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**NEW SPECIES AND NEW RECORDS OF CLOACINA VON LISTOW, 1898
(NEMATODA: STRONGYLOIDEA) PARASITIC IN MACROPODID
MARSUPIALS FROM PAPUA NEW GUINEA**

I. BEVERIDGE

Summary

New species described from macropodid marsupials in Papua New Guinea are : *Cloacina cretheis* sp. nov. from tree kangaroos, *Dendrolagus inustus* (type host), *D. dorianus*, *D. goodfellowi*, *D. matchiei* and *D. scottae*; *C. cunctabunda* sp. nov. from *D. mbaiso*; *C. eurynome* sp. nov. from *D. dorianus* and *D. scottae*; *C. hecale* sp. nov. from *D. dorianus*; *C. theope* sp. nov. from *D. matschiei* and *D. dorianus*; *C. erigone* sp. nov., *C. hyperaea* sp. nov., *C. nephele* sp. nov., *C. polymena* sp. nov., *C. praxithea* sp. nov. and *C. procris* sp. nov. from the scrub wallaby, *Macropus agilis*. New host records are : *C. caballeroi* Mawson, 1977, *C. sterope* Beveridge & Speare, 1999 and *C. syphax* Beveridge & Speare, 1999 in *Do. Hageni*. Additional geographical records are given for *C. cornuta* in *M. agilis*. A key to the known species of *Cloacina* in Papua New Guinea is provided.

NEW SPECIES AND NEW RECORDS OF *CLOACINA* VON LINSTOW, 1898
(NEMATODA: STRONGYLOIDEA) PARASITIC IN MACROPODID
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BEVERIDGE, I. 2002. New species and new records of *Cloacina* von Linstow, 1898 (Nematoda: Strongyloidea) parasitic in macropodid marsupials from Papua New Guinea. *Records of the South Australian Museum* 35(1): 1–32.

New species described from macropodid marsupials in Papua New Guinea are : *Cloacina cretheis* sp. nov. from tree kangaroos, *Dendrolagus inustus* (type host), *D. dorianus*, *D. goodfellowi*, *D. matschiei* and *D. scottae*; *C. cunctabunda* sp. nov. from *D. mbaiso*; *C. eurynome* sp. nov. from *D. dorianus* and *D. scottae*; *C. hecale* sp. nov. from *D. dorianus*; *C. theope* sp. nov. from *D. matschiei* and *D. dorianus*; *C. erigone* sp. nov., *C. hyperaea* sp. nov., *C. nephele* sp. nov., *C. polymena* sp. nov., *C. praxitheia* sp. nov. and *C. procris* sp. nov. from the scrub wallaby, *Dorcopsis hageni*, and *C. oweni* n. sp. and *C. papuensis* n. sp. from the agile wallaby, *Macropus agilis*. New host records are: *C. caballeroi* Mawson, 1977, *C. sterope* Beveridge & Speare, 1999 and *C. syphax* Beveridge & Speare, 1999 in *D. hageni*. Additional geographical records are given for *C. cornuta* in *M. agilis*. A key to the known species of *Cloacina* in Papua New Guinea is provided.

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Species of the nematode genus *Cloacina* von Linstow, 1898 occur exclusively in the stomachs of macropodid marsupials. Currently, 103 species are recognised as valid (Beveridge 1998, 1999; Beveridge and Speare 1999) although substantial numbers of species remain to be described (Beveridge 1998). Most of the species described to date are from Australian kangaroos and wallabies, with relatively few records from Papua New Guinea. This situation reflects the paucity of knowledge of the parasite fauna of macropodids from Papua New Guinea, which is based currently on a small number of incidental collections. Nevertheless, material currently available from various kangaroos and wallabies consists of a number of novel species of *Cloacina*. Thirteen new species are described in the current paper as well as new host and distribution records. The opportunity is taken to provide a summary of species of *Cloacina* known from Papua New Guinea together with a key to facilitate their identification. Finally, a preliminary comparison is made between the Australian and Papua New Guinean species and their host distributions.

Beveridge (1998) noted the occurrence of a number of species of *Cloacina* in Papua New Guinea, specifically *C. australis* (Yorke & Maplestone, 1926) in the agile wallaby, *Macropus agilis* (Gould, 1842); *C. caballeroi* Mawson, 1977

in the grey scrub wallaby, *Dorcopsis luctuosa* (D'Alberty, 1874) and the brown scrub wallaby, *D. muelleri* (Schlegel, 1866); *C. cloelia* Beveridge, 1998 in the pademelons *Thylogale calabyi* Flannery, 1992 and *T. stigmatica* (Gould, 1860); *C. cornuta* (Davey & Wood, 1938) in *M. agilis*; *C. cybele* Beveridge, 1998 in *T. stigmatica*; and *C. dahli* von Linstow, 1898 in *Thylogale browni* Ramsay, 1877, *T. calabyi* and *T. stigmatica*. Subsequently, based on an examination of the parasites of four small scrub wallabies, *Dorcopsulus vanheurni* (Thomas, 1922), Beveridge & Speare (1999) described seven new species, *C. sancus*, *C. sciron*, *C. sappho*, *C. solon*, *C. solymus*, *C. sterope* and *C. syphax*. Beveridge (1998) noted the presence of undescribed species from the white-striped scrub wallaby, *Dorcopsis hageni* Heller, 1897 in the collections of the South Australian Museum, Adelaide, and from *D. luctuosa* in the collections of The Natural History Museum, London. Flannery et al. (1996) also reported species of the genus *Cloacina* in a variety of tree kangaroos: *Dendrolagus inustus* Mueller, 1840; *D. goodfellowi* Thomas, 1908; *D. dorianus* Ramsay, 1883; *D. scottae* Flannery & Seri, 1990; and *D. mbaiso* Flannery, Boeadi & Szalay, 1995, a group of kangaroos not previously known to harbour *Cloacina*. These various undescribed collections form the basis of the current report.

MATERIALS AND METHODS

Nematodes were examined from collections held in the Australian Helminthological Collection (AHC), South Australian Museum (SAM), Adelaide, the Natural History Museum (BMNH), London and the United States National Parasite Collection (USNPC), Beltsville, Maryland. Nematodes were washed in water and cleared in lactophenol. Drawings were made using a drawing tube attached to an Olympus BH2 microscope. Drawings of apical views of the heads of nematodes are oriented with the dorsal aspect uppermost; drawings of the bursa have the ventral surface uppermost. All drawings are of paratype specimens. Measurements were made with an ocular micrometer. All measurements are in millimetres and are presented as the range followed by the mean in parentheses.

Morphological terminology follows Beveridge (1998). Because of the relative uniformity of the genus *Cloacina*, the descriptions presented are abbreviated and follow the format used by Beveridge (1998), in which a full description of the genus was followed by individual species descriptions concentrating on features of diagnostic significance. A detailed description of the genus is available in Beveridge (1998). Features which are relatively invariable, such as the disposition of ventral and lateral bursal rays, are not included in descriptions but are, nonetheless, illustrated.

Types of the new species have been deposited in SAM, BMNH and USNPC. Host nomenclature follows Flannery (1995) and Flannery et al. (1995).

Following previous practice (Beveridge 1998), the names of new species are based on those of classical deities since *Cloacina* was the Roman goddess of the toilet. An invocational quatrain on this subject, usually attributed to Byron (see Lewin 1999, p. 31), occurs in a number of variations, but the rendering by Lewin (1999) is presented here:

O *Cloacina*, goddess of this place,
Look on thy suppliants with smiling face,
Soft yet cohesive let their offerings flow,
Not rashly swift nor insolently slow.

SYSTEMATICS

Cloacina caballeroi Mawson, 1977

Material examined: 7♂, 13♀, from stomach of

Dorcopsis hageni, Usino, Madang, Papua New Guinea, coll. T. Reardon, May 1987, SAM AHC 31425.

Remarks

Cloacina caballeroi was described by Mawson (1977) and Beveridge (1998) from *Dorcopsis muelleri* and *Do. luctuosa* from Irian Jaya and Papua New Guinea. This represents the first record from *Do. hageni*.

Cloacina cornuta (Davey & Wood, 1938)

Material examined: 2♂, 1♀, from stomach of *Macropus agilis*, Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998, BMNH 1998.9.28.24–26.

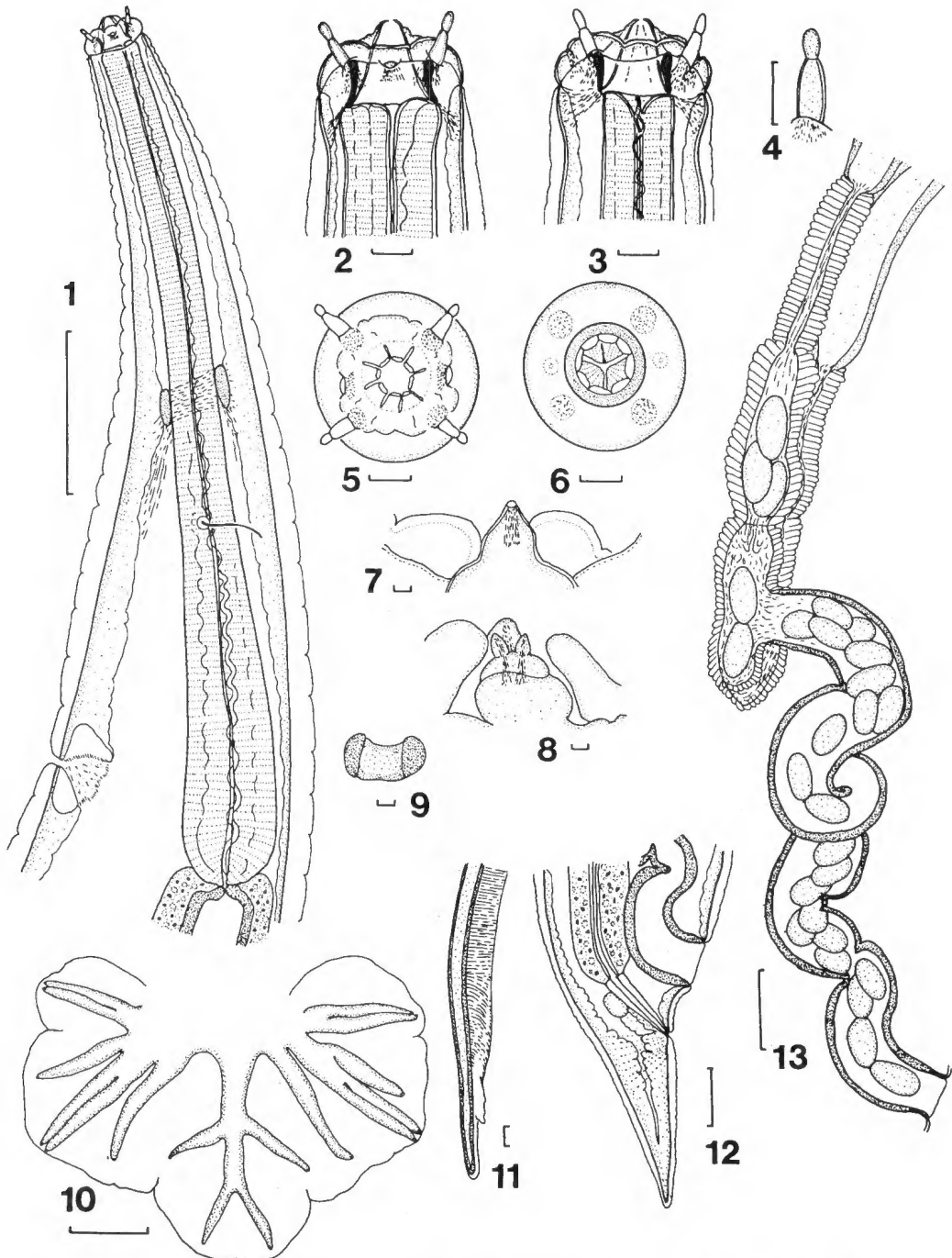
Remarks

Cloacina cornuta was reported from *Macropus agilis* from Port Moresby and Cape Rodney by Beveridge (1998). The present record adds an additional locality. Data provided by Dr I. Owen indicate that in four wallabies examined, numbers of *C. cornuta* ranged from 1650–9600 (mean 4700). Although based on a very small number of wallabies, these data contrast strikingly with those of Speare et al. (1983) for *M. agilis* from northern Australia in which *C. cornuta* was found in only 41% of hosts examined, and with Beveridge et al. (1998) who found the nematode in 35% of wallabies in Queensland. In Australia, *C. cornuta* invariably occurs in much lower numbers than the synhospitalic species *C. australis* (unpublished observations).

Cloacina cretheis sp. nov.
(Figs 1–13)

Types: From stomach of *Dendrolagus inustus*, Mt Somoro, Sandaun Province, Papua New Guinea, coll. T. Flannery, 10.iii.1990. Holotype ♂, SAM AHC 31426; allotype ♀, SAM AHC 31427. Paratypes: 12♂, 12♀, SAM AHC 31428; 1♂, 1♀, BMNH 2001.4.10.1–2; 1♂, 1♀, USNPC 91133. Slide preparations of male, apical views of mouth and bursa, SAM AHC 28378.

Material examined: From *Dendrolagus inustus*: types. From *Dendrolagus dorianus*: 1♂, 4♀, Gunung Ki, Tembagapura, Irian Jaya, coll. T. Flannery, 19.v.1994, SAM AHC 31430; 2♂, 10♀, Lake Trist, Papua New Guinea, coll. I. Redmond, BMNH, 1979, 4486–4505. From *Dendrolagus*



FIGURES 1–13. *Cloacina cretheis* sp. nov., specimens from *Dendrolagus inustus*. 1. Anterior end, lateral view. 2. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 3. Cephalic extremity, dorsal view. 4. Submedian cephalic papilla. 5. Cephalic extremity, apical view. 6. Cephalic extremity, transverse optical section through buccal capsule. 7. Genital cone, ventral view. 8. Genital cone, dorsal view. 9. Gubernaculum, ventral view. 10. Bursa, apical view. 11. Distal tip of spicule, lateral view. 12. Female tail, lateral view. 13. Female genital system, lateral view. Scale bars: 1, 10, 12, 13, 0.1 mm; 2–9, 11, 0.01 mm.

goodfellowi: 5♂, 5♀, Mt Machold, Sandaun Province, Papua New Guinea, coll. T. Flannery and K. Vula, 13.xii.1990, SAM AHC 31431. From *Dendrolagus matschiei* Forster & Rothschild, 1907: 26♂, 28♀, Huon Peninsula, Papua New Guinea, coll. J. Mayer, July 1999, USNPC 91146. From *Dendrolagus scottae*: 9♂, 5♀, Sweipini, Sandaun Province, Papua New Guinea, coll. T. Flannery, 15.vi.1991, SAM AHC 31429.

Description

Small nematodes; cervical cuticle very slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.015 long, projecting anteriorly from peri-oral cuticle; distal segment sub-spherical, 0.005 long, shorter than cylindrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus slender, claviform, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 6.7–9.0 (7.8); maximum width 0.35–0.45 (0.40); buccal capsule 0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.46–0.57 (0.52); nerve ring to anterior end 0.20–0.24 (0.22); excretory pore to anterior end 0.39–0.48 (0.45); deirid to anterior end 0.28–0.36 (0.32); spicules 2.34–2.62 (2.54); gubernaculum 0.03 (0.03) long.

Measurements of 5 specimens from *D. goodfellowi*: total length 7.9–9.3 (8.8); maximum width 0.48–0.56 (0.51); buccal capsule 0.010–0.012 (0.011) x 0.023–0.025 (0.023); oesophagus 0.53–0.64 (0.59); nerve ring to anterior end 0.23–0.24 (0.24); excretory pore to anterior end 0.44–0.53 (0.47); deirid to anterior end 0.20–0.34 (0.29); spicules 2.53–2.94 (2.74); gubernaculum 0.030–0.040 (0.034) long.

Measurements of 3 specimens from *D. scottae*: total length 6.9–9.7 (8.4); maximum width 0.43–0.47 (0.45); buccal capsule 0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.48–0.62 (0.56);

nerve ring to anterior end 0.20; excretory pore to anterior end 0.40–0.46 (0.42); deirid to anterior end 0.25–0.31 (0.28); spicules 2.63–2.66 (2.65); gubernaculum 0.030–0.035 (0.032) long.

Measurements of single specimens from *D. dorianus*: total length 9.4; maximum width 0.43; buccal capsule 0.010 x 0.025; oesophagus 0.50; excretory pore to anterior end 0.50; deirid to anterior end 0.26; spicules 2.97; gubernaculum 0.035 long.

Dorsal ray elongate; external branchlets arise at 1/3 length, before major bifurcation; angle of bifurcation acute; external branchlets as long as internals, directed postero-laterally, not reaching margin of bursa; internal branchlets originate 2/3 along dorsal ray, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip blunt; ala terminates anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 7.7–9.0 (8.2); maximum width 0.52–0.54 (0.52); buccal capsule 0.008–0.010 (0.010) x 0.023–0.025 (0.023); oesophagus 0.48–0.55 (0.53); nerve ring to anterior end 0.20–0.30 (0.23); excretory pore to anterior end 0.39–0.50 (0.44); deirid to anterior end 0.26–0.33 (0.30); tail 0.23–0.31 (0.27); vulva to posterior end 0.35–0.40 (0.38); vagina 0.50–0.73 (0.62); egg 0.075–0.080 (0.080) x 0.040–0.050 (0.045).

Measurements of 5 specimens from *D. scottae*: total length 8.8–10.7 (10.0); maximum width 0.49–0.64 (0.59); buccal capsule 0.008–0.010 (0.009) x 0.020–0.025 (0.023); oesophagus 0.53–0.58 (0.55); nerve ring to anterior end 0.20; excretory pore to anterior end 0.48–0.50 (0.49); deirid to anterior end 0.29–0.32 (0.30); tail 0.23–0.32 (0.28); vulva to posterior end 0.38–0.40 (0.39); vagina 0.53–0.58 (0.56).

Measurements of 3 specimens from *D. dorianus*: total length 8.8–9.2 (9.0); maximum width 0.49–0.72 (0.60); buccal capsule 0.010–0.013 (0.012) x 0.023–0.025 (0.024); oesophagus 0.53–0.60 (0.57); nerve ring to anterior end 0.23 (0.23); excretory pore to anterior end 0.48–0.51 (0.49); deirid to anterior end 0.20–0.29 (0.24); tail 0.21–0.25 (0.23); vulva to posterior end 0.49–0.50 (0.49); vagina 0.64–0.67 (0.66); egg 0.070–0.075 (0.078) x 0.040–0.050 (0.045).

Female tail short, conical; vagina elongate, convoluted; egg ellipsoidal.

Remarks

C. cretheis sp. nov. is characterised by submedian papillae with a small sub-spherical distal segment, a simple buccal capsule, eight elements to the leaf crown, a slender, unornamented oesophagus, deirids posterior to the nerve ring, a dorsal ray in which the external branchlets arise before the major bifurcation and an elongate, convoluted vagina. The shape of the dorsal ray alone separates it from all congeners except *C. caballeroi*, *C. enyo* Beveridge, 1998, *C. ips* Beveridge, 1998, and *C. syphax*. It differs from all of these except *C. caballeroi* in having the deirid posterior to the nerve ring, although in some highly contracted specimens of *C. cretheis*, in which the anterior oesophagus becomes sinuous, the deirid may appear more anteriorly on the contracted cuticle. *C. cretheis* is further distinguished from *C. syphax* which has a sinuous anterior margin to its buccal capsule and submedian cephalic papillae with enlarged distal segments. *C. cretheis* is distinguished from *C. caballeroi* by spicule lengths, which are 2.34–2.97 mm in *C. cretheis* compared with 1.23–1.45 mm in *C. caballeroi*. The spicules of *C. enyo* are 0.68–0.88 mm long while those of *C. ips* are 1.36–1.39 mm in length, providing a further means of distinguishing the latter species.

C. cretheis occurs in a wide range of tree kangaroo species in Papua New Guinea and was by far the most frequently encountered species in tree kangaroos in this study. It does not occur in either *Dendrolagus bennettianus* DeVis, 1887 or *D. lumholtzi* Collett, 1884 in Australia (Spratt et al. 1991). Although incomplete, the measurements of specimens from different hosts suggest that there are no major differences induced by the host species. Some of the minor differences observed are due to the state of contraction or of preservation of specimens, and the incomplete sets of measurements reflect the poor state of preservation of many of the specimens, precluding the measurement of internal organs.

Cloacina cunctabunda sp. nov.
(Figs 14–23)

Types: From stomach of *Dendrolagus mbaio*, Camp Ridge, Tembagapura, Irian Jaya, coll. T. Flannery, 24.v.1994. Holotype ♂, SAM AHC 31432; allotype ♀, SAM AHC 31433. Paratype ♂, 3 slides, SAM AHC 28379.

Description

Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.010 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.006 long, longer than cylindrical proximal segment, 0.004 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, oval in transverse section, slightly deeper dorso-ventrally, wider than deep, wall without striations. Leaf crown elements 6 in number, recurved at tips; peri-oral cuticle, inflated; inflations not attached to each element of leaf crown. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus slender, claviform, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in mid-oesophageal region; deirids anterior to nerve ring, mid-way between nerve ring and buccal capsule; excretory pore anterior to level of oesophago-intestinal junction.

Male. Measurements of holotype and paratype. Total length 3.30, 3.32; maximum width 0.16, 0.17; buccal capsule 0.008, 0.010 x 0.025, 0.025; oesophagus 0.34, 0.35; nerve ring to anterior end 0.16, 0.18; excretory pore to anterior end 0.26, 0.30; deirid to anterior end 0.11, 0.14; spicules 1.39, 1.57; gubernaculum 0.015, 0.015 long.

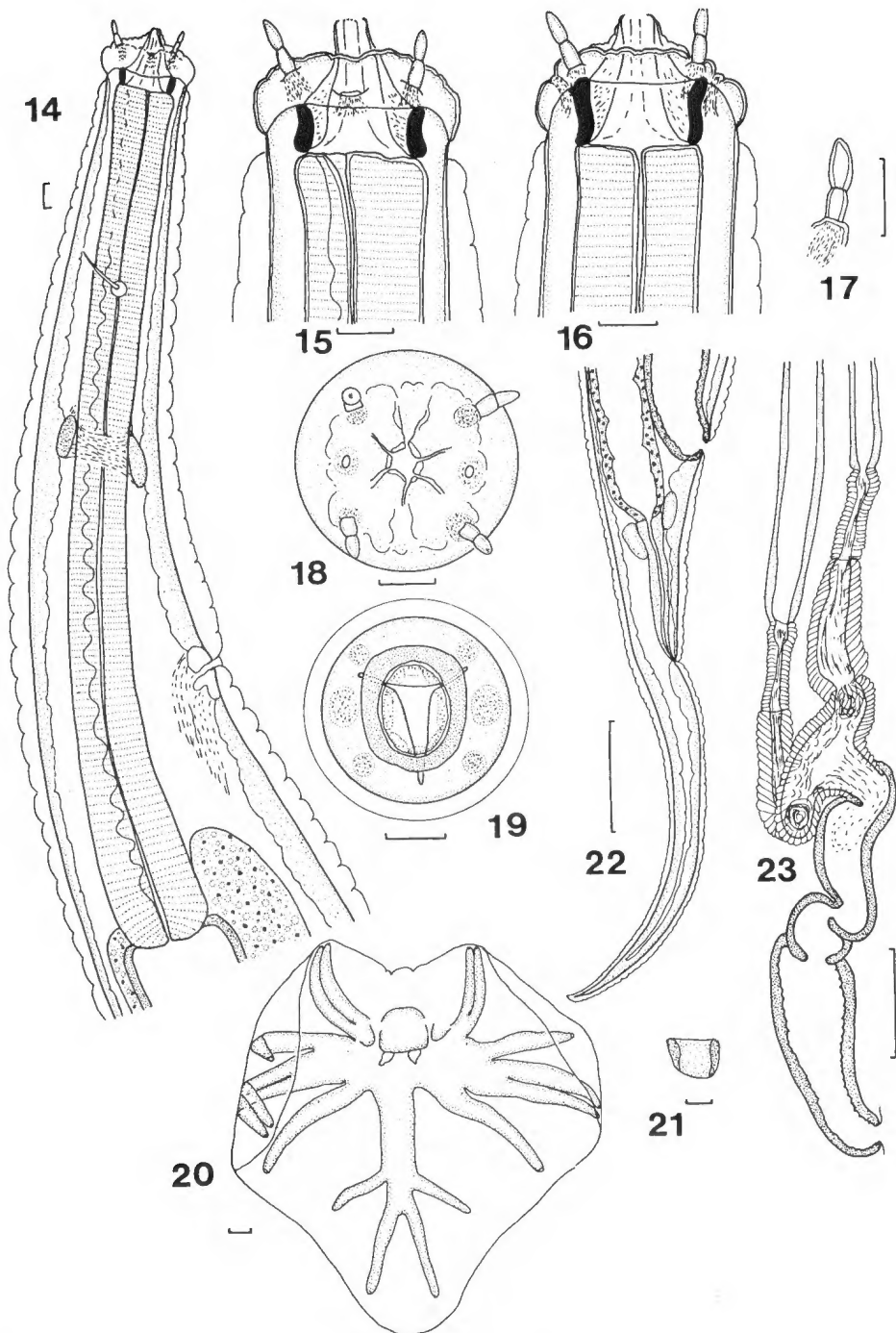
Dorsal lobe of bursa and dorsal ray elongate, ray broad at origin; external branchlets arise at 1/2 length, immediately before major bifurcation; angle of bifurcation acute; external branchlets shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets originate soon after externals arise from dorsal ray, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip not everted. Anterior lip of genital cone conical; posterior lip with paired projections.

Female. Measurements of allotype. Total length 4.25; maximum width 0.21; buccal capsule 0.010 x 0.025; oesophagus 0.40; nerve ring to anterior end 0.18; excretory pore to anterior end 0.29; deirid to anterior end 0.11; tail 0.35; vulva to posterior end 0.55; vagina 0.35.

Female tail elongate, conical; vulva immediately anterior to anus; vagina short with single convolution; egg not seen.

Remarks

Although described from only three specimens,



FIGURES 14–23. *Cloacina cunctabunda* sp. nov., specimens from *Dendrolagus mbaiso*. 14. Anterior end, lateral view. 15. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 16. Cephalic extremity, ventral view. 17. Submedian cephalic papilla, lateral view. 18. Cephalic extremity, apical view. 19. Cephalic extremity, transverse optical section through buccal capsule. 20. Bursa, apical view. 21. Gubernaculum, ventral view. 22. Female tail, lateral view. 23. Female genital system, lateral view. Scale bars: 22, 23, 0.1 mm; 14–21 0.01 mm.

this species is sufficiently distinctive to allow ready recognition, and comes from a host restricted to isolated localities in Irian Jaya which is unlikely to be sampled extensively in the future (Flannery et al. 1995). Furthermore, this species of *Cloacina* was not found in any other species of tree kangaroo.

C. cunctabunda is distinguished from all congeners except *C. cretheis*, *C. caballeroi*, *C. enyo*, *C. ips* and *C. syphax* in possessing a simple buccal capsule, an elongate, unornamented oesophagus and the external branchlets of the dorsal ray arising before the major bifurcation. The position of the deirid anterior to the nerve ring distinguishes the species from *C. cretheis* and *C. caballeroi*, while the shape of the buccal capsule and the submedian cephalic papillae distinguish it from *C. syphax*. *C. cunctabunda* is distinguished from *C. enyo* on the basis of spicule lengths, which are 1.39–1.57 mm long in *C. cunctabunda* compared with 0.68–0.88 mm in *C. enyo*. *C. cunctabunda* therefore most closely resembles *C. ips*, from which it is distinguished by the number of leaf crown elements (six in *C. cunctabunda*, eight in *C. ips*), in the absence of a dorsal oesophageal tooth which projects prominently into the buccal capsule of *C. ips*, in the shape of the female tail which is slender and elongate in *C. cunctabunda* but short and conical in *C. ips*, and in the shape of the vagina which is straight in *C. ips* but convoluted in *C. cunctabunda*.

Cloacina erigone sp. nov.
(Figs 24–36)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May 1987. Holotype ♂, SAM AHC 31434; allotype ♀, SAM AHC 31435. Paratypes: 4♂, 5♀, SAM AHC 31436, 1♂, 1♀, BMNH 2001.4.10.3–4, 1♂, 1♀, USNPC 91134. Slide preparations of apical views of mouth and bursa, SAM AHC 28380.

Material examined: types.

Description

Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.013 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.005 long, shorter than cylindrical proximal

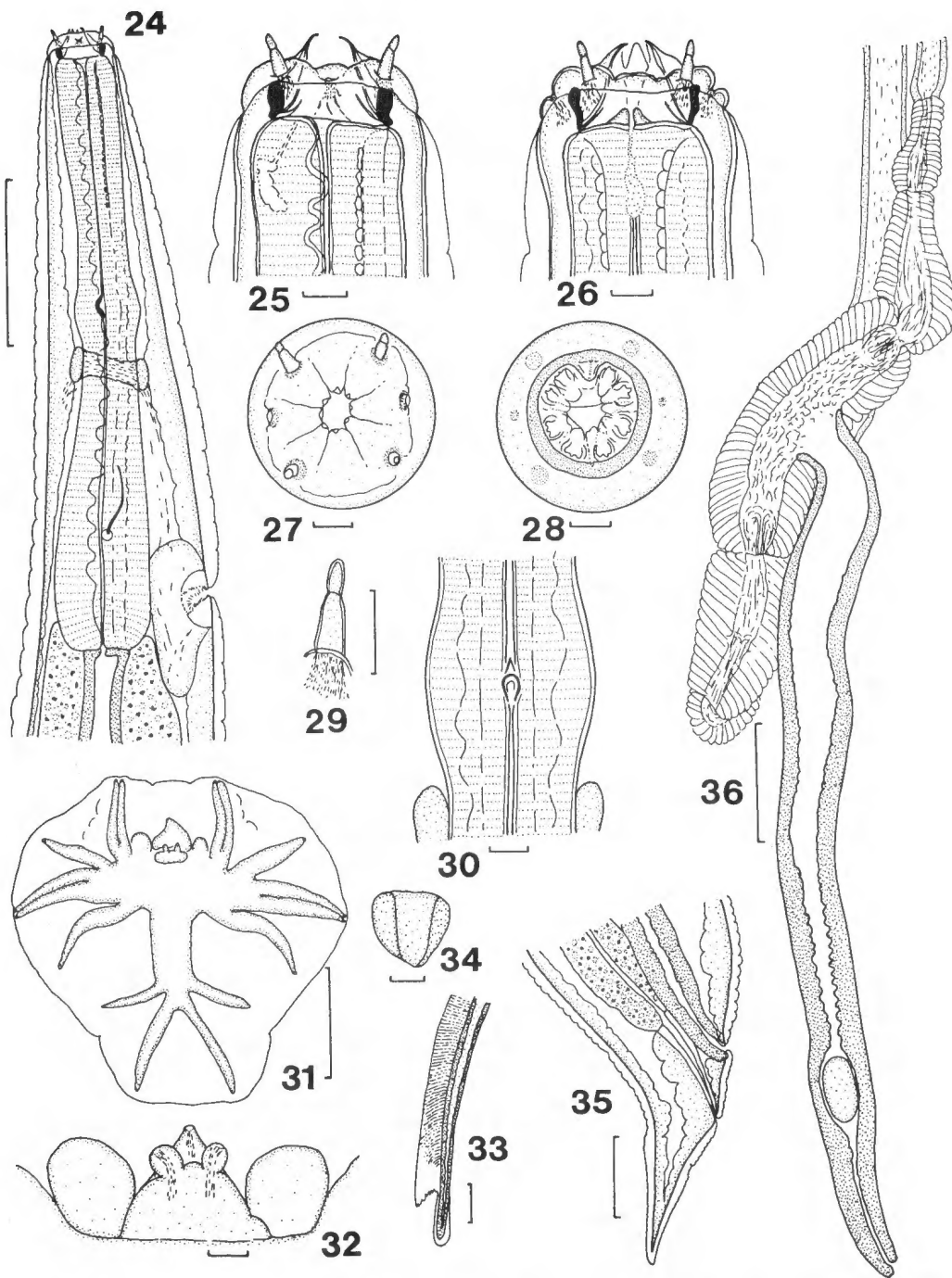
segment, 0.008 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips, margins prominently thickened; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule. Oesophagus claviform, robust, slightly wider at posterior end; lining with sclerotised bosses extending from anterior end, halfway to nerve ring; single dorsal denticle present in prominent preneural swelling of oesophagus. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring, almost at level of excretory pore; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 8 specimens, types. Total length 2.88–5.11 (4.02); maximum width 0.18–0.31 (0.26); buccal capsule 0.007–0.010 (0.008) x 0.023–0.035 (0.032); oesophagus 0.26–0.39 (0.34); nerve ring to anterior end 0.14–0.22 (0.18); excretory pore to anterior end 0.25–0.40 (0.33); deirid to anterior end 0.23–0.37 (0.32); spicules 1.35–1.79 (1.59); gubernaculum 0.020–0.030 (0.024) long.

Dorsal ray elongate, broad at origin; external branchlets arise at 1/2 length, immediately before major bifurcation; angle of bifurcation acute; external branchlets shorter than internals, directed laterally, not reaching margin of bursa; internal branchlets originate immediately after externals, directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 8 specimens, types. Total length 3.56–4.81 (4.39); maximum width 0.31–0.48 (0.41); buccal capsule 0.008–0.010 (0.009) x 0.033–0.045 (0.039); oesophagus 0.35–0.44 (0.39); nerve ring to anterior end 0.16–0.23 (0.20); excretory pore to anterior end 0.21–0.43 (0.34); deirid to anterior end 0.26–0.37 (0.32); tail 0.16–0.19 (0.17); vulva to posterior end 0.24–0.28 (0.26); vagina 0.53–0.99 (0.75); egg 0.055–0.070 (0.062) x 0.030–0.035 (0.031).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, straight; egg ellipsoidal.



FIGURES 24–36. *Cloacina erigone* sp. nov., types. 24. Anterior end, lateral view. 25. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 26. Cephalic extremity, dorsal view. 27. Cephalic extremity, apical view. 28. Cephalic extremity, transverse optical section through buccal capsule. 29. Submedian cephalic papilla, lateral view. 30. Preneural oesophageal swelling showing dorsal denticle, dorsal view. 31. Bursa, apical view. 32. Genital cone, dorsal view. 33. Spicule tip, lateral view. 34. Gubernaculum, ventral view. 35. Female tail, lateral view. 36. Female genital system, lateral view. Scale bars: 24, 31, 35, 36, 0.1 mm; 25–30, 32–34, 0.01 mm.

Remarks

Cloacina erigone sp. nov. is characterised by having submedian cephalic papillae with an elongate proximal segment, a shallow, unornamented buccal capsule, eight leaf crown elements, deirid posterior to the nerve ring, a dorsal ray with the external branchlets arising before the main bifurcation and a straight vagina. In these characters, *C. erigone* resembles *C. caballeroi*, *C. cretheis*, *C. enyo*, *C. ips* and *C. syphax*. It differs from all of these species, however, in having bosses lining the anterior part of the vagina and a single dorsal denticle. Species with a symmetrical buccal capsule, oesophageal bosses and a single dorsal denticle are *C. australis*, *C. dis* Beveridge, 1998, *C. hecuba* Beveridge, 1998, *C. io* Beveridge, 1998, *C. laius*, *C. leto* Beveridge, 1998, *C. minor* (Davey & Wood, 1938) and *C. tyro* Beveridge, 1998. However, in none of these species is the deirid posterior to the nerve ring, and in none do the external branchlets of the dorsal ray arise before the principal bifurcation.

This species has, thus far, been found only in *Do. hageni*.

Cloacina eurynome sp. nov.

(Figs 37–49)

Types: From stomach of *Dendrolagus dorianus*, Tembagapura, Irian Jaya, coll. T. Flannery, 19.v.1994, 23.v.1994. Holotype ♂, SAM AHC 31437; allotype ♀, SAM AHC 31438. Paratypes: 4♂, 9♀, SAM AHC 31439, 1♂, 2♀, SAM AHC 31440, 1♂, 1♀, BMNH 2001.4.10.5–6, 1♂, 1♀, USNPC 91135. Slide preparations of spicules, apical views of mouth and bursa, SAM AHC 28381.

Material examined: From *Dendrolagus dorianus*: types. From *Dendrolagus scottae*: 4♀, Sweipini, Sandaun Province, Papua New Guinea, coll. T. Flannery, 15.vi.1991, SAM AHC 31441.

Description

Small nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.018 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, pointed apically, 0.008 long, shorter than cylindrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrical in dorsal and lateral views, approximately octagonal in transverse section,

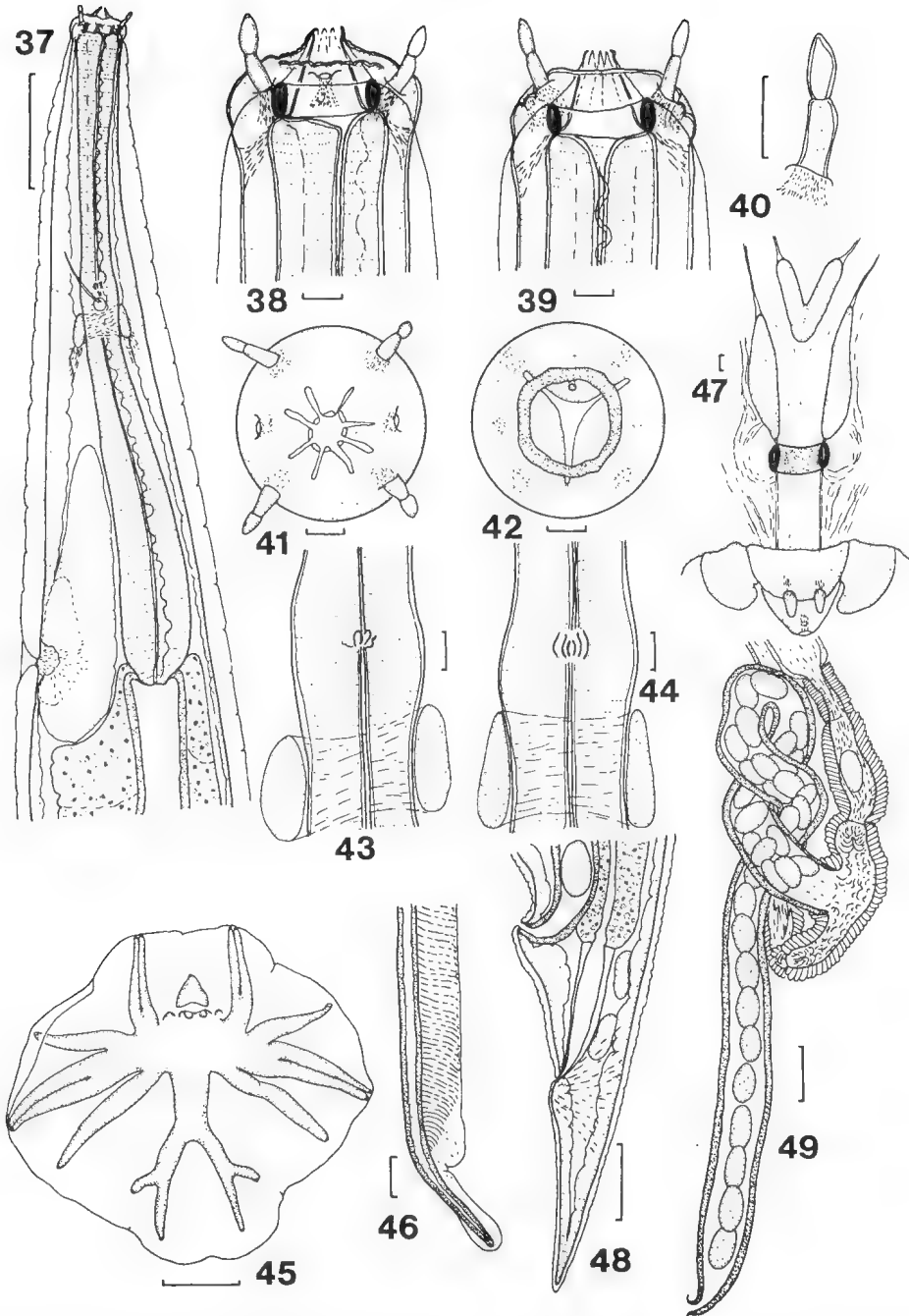
wider than deep, wall without striations. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender, only slightly wider at posterior end; lining without sclerotised bosses; three poorly developed denticles, one dorsal and two subventral, present in lumen of oesophagus immediately anterior to nerve ring; preneural swelling of oesophagus small. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 7 specimens, types. Total length 8.75–10.67 (9.53); maximum width 0.39–0.48 (0.45); buccal capsule 0.007–0.010 (0.008) x 0.027–0.030 (0.029); oesophagus 0.57–0.64 (0.59); nerve ring to anterior end 0.26–0.28 (0.27); excretory pore to anterior end 0.54–0.62 (0.58); deirid to anterior end 0.24–0.32 (0.28); spicules 3.57–3.98 (3.77); gubernaculum 0.015–0.020 (0.019) long.

Dorsal ray elongate, broad at origin; major bifurcation occurs at 1/3 length; angle of bifurcation acute; external branchlets arise midway between major bifurcation and tip, much shorter than internals, directed laterally or postero-laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule tip blunt, gently curved; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 10.19–13.28 (11.50); maximum width 0.52–0.75 (0.60); buccal capsule 0.005–0.013 (0.008) x 0.030–0.035 (0.031); oesophagus 0.61–0.73 (0.65); nerve ring to anterior end 0.25–0.28 (0.27); excretory pore to anterior end 0.52–0.71 (0.60); deirid to anterior end 0.18–0.34 (0.27); tail 0.22–0.29 (0.25); vulva to posterior end 0.31–0.46 (0.39); vagina 1.57–1.85 (1.75); egg 0.080–0.095 (0.086) x 0.040–0.050 (0.046).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, straight distally, recurrent anterior to vestibule, recurrent section twisted in characteristic figure of eight formation; egg ellipsoidal.



FIGURES 37–49. *Cloacina eurynome* sp. nov., types. 37. Anterior end, lateral view. 38. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 39. Cephalic extremity, ventral view. 40. Submedian cephalic papilla, lateral view. 41. Cephalic extremity, apical view. 42. Cephalic extremity, transverse optical section through buccal capsule. 43. Preneural oesophageal swelling showing denticles, lateral view, dorsal aspect on right-hand side. 44. Preneural oesophageal swelling showing denticles, ventral view. 45. Bursa, apical view. 46. Spicule tip, lateral view. 47. Gubernaculum, genital cone and thickenings of spicule sheaths, dorsal view. 48. Female tail, lateral view. 49. Female genital system, lateral view. Scale bars: 37, 45, 48, 49, 0.1 mm; 38–44, 46, 47, 0.01 mm.

Remarks

The presence of three preneural denticles at the same level in the oesophagus distinguishes *C. eurynome* from all congeners except *C. hera* Beveridge, 1998, *C. hermes* Beveridge, 1998 and *C. hestia* Beveridge, 1998, all of which are parasites of grey kangaroos, *Macropus fuliginosus* (Desmarest, 1817) and *M. giganteus* Shaw, 1790 in eastern and southern Australia (Beveridge 1998) and *C. daveyi* Mawson, 1977 in the wallaroo, *M. robustus* Gould, 1841. *C. eurynome* is distinguished from the species in grey kangaroos in having the deirid at the level of the nerve ring rather than well anterior to it and in having eight rather than six leaf crown elements. It is distinguished from *C. daveyi* which has cephalic papillae with large, globose, medially directed distal segments. The denticles in *C. eurynome* are vestigial, a feature found only in *C. hestia*. *C. eurynome* is distinguished from all congeners other than *C. syphax*, from *Dorcopsulus vanheurni*, also from Papua New Guinea, in the morphology of the vagina, which exhibits a highly characteristic recurrent loop, anterior to the vestibule, twisted in a figure of eight formation. *C. eurynome* differs from *C. syphax* in possessing denticles, in having a straight rather than a sinuous anterior margin to the buccal capsule, and in having the external branchlets of the dorsal ray arise after the major bifurcation.

Cloacina hecale sp. nov. (Figs 50–61)

Types: From stomach of *Dendrolagus dorianus*, Lake Trist, Papua New Guinea, coll. I. Redmond, 1979. Holotype ♂, BMNH 1981.4506; allotype ♀, BMNH 1981.4507. Paratypes: 49♂, 88♀, BMNH 1981.4508–4535. Slide preparations of apical views of bursa and mouth, SAM AHC 28383.

Material examined: From *Dendrolagus dorianus*: types.

Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.023 apart. Submedian cephalic papillae prominent, 0.017 long, projecting anteriorly from peri-oral cuticle; distal segment conical, 0.007 long, only slightly shorter than cylindrical proximal segment, 0.010 long. Buccal capsule

shallow, symmetrical in dorsal and lateral views, circular in transverse section, wider than deep, wall without striations; anterior margin slightly undulant. Leaf crown elements 8 in number, slightly recurved at tips; peri-oral cuticle not inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender, slightly wider at posterior end; lining without sclerotised bosses; denticles absent. Nerve ring in anterior oesophageal region; deirids anterior to nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 9.44–13.86 (11.82); maximum width 0.50–0.67 (0.60); buccal capsule 0.010–0.013 (0.011) x 0.035–0.040 (0.039); oesophagus 0.76–0.95 (0.87); nerve ring to anterior end 0.30–0.32 (0.31); excretory pore to anterior end 0.52–0.98 (0.80); deirid to anterior end 0.17–0.26 (0.23); spicules 3.90–5.05 (4.54); gubernaculum 0.040 long.

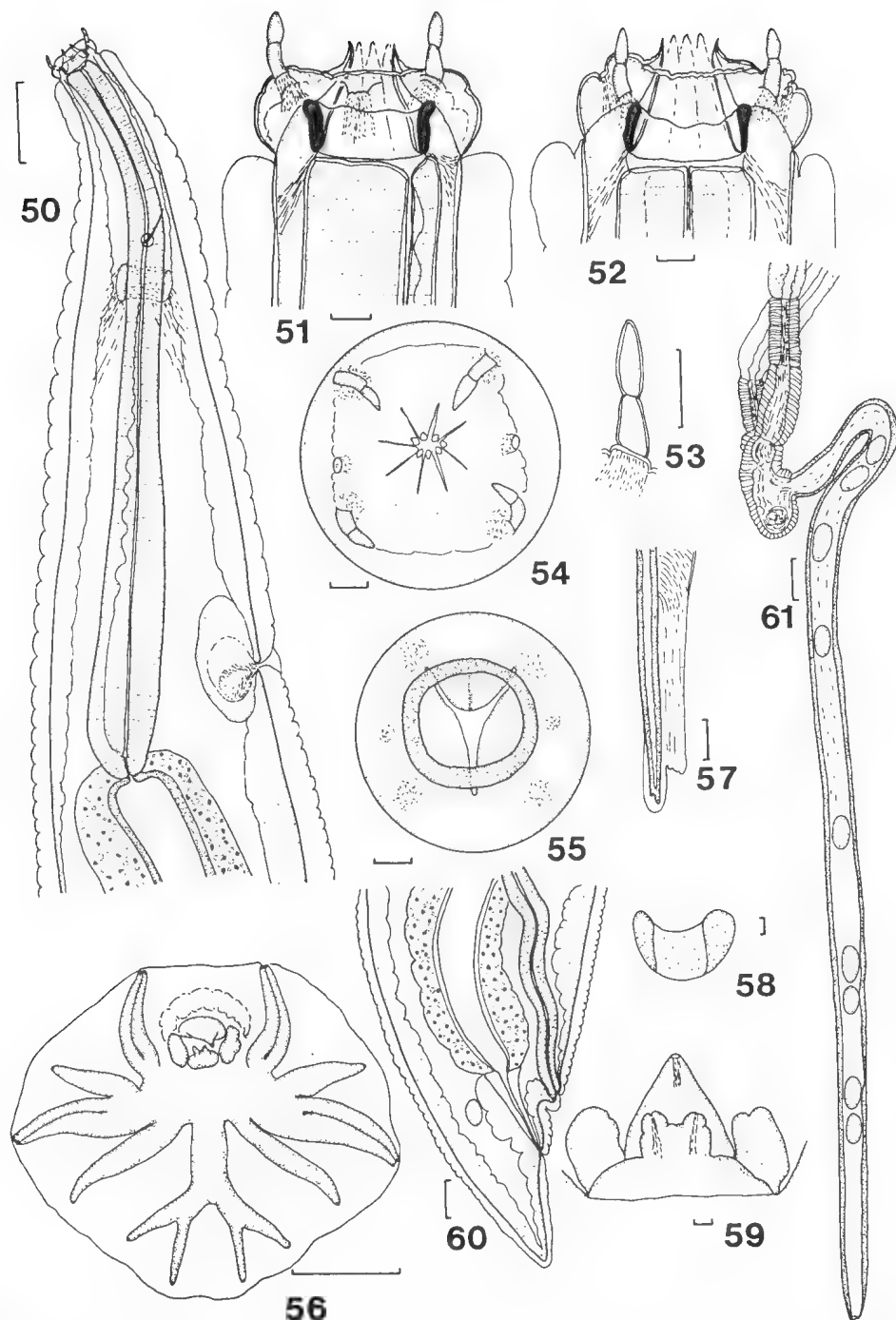
Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; external branchlets arise immediately after major bifurcation, as long as internals, though more robust, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, wider than long. Spicule minutely bifid at tip; ala terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 19.6–22.9 (21.3); maximum width 0.64–0.91 (0.81); buccal capsule 0.010 (0.010) x 0.040 (0.040); oesophagus 0.95–1.02 (0.97); nerve ring to anterior end 0.25–0.29 (0.27); excretory pore to anterior end 0.63–0.86 (0.70); deirid to anterior end 0.19–0.29 (0.22); tail 0.13–0.30 (0.21); vulva to posterior end 0.18–0.43 (0.28); vagina 2.22–2.57 (2.40); vestibule 0.27; sphincter 0.22; infundibulum 0.17; egg 0.090–0.110 (0.096) x 0.045–0.050 (0.048).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, straight, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina hecale sp. nov. is a robust species characterised by long spicules and an elongate



FIGURES 50-61. *Cloacina hecale* sp. nov., types. 50. Anterior end, lateral view. 51. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 52. Cephalic extremity, dorsal view. 53. Submedian cephalic papilla, lateral view. 54. Cephalic extremity, apical view. 55. Cephalic extremity, transverse optical section through buccal capsule. 56. Bursa, apical view. 57. Spicule tip, lateral view. 58. Gubernaculum, ventral view. 59. Genital cone, dorsal view. 60. Female tail, lateral view. 61. Female genital system, lateral view. Scale bars: 50, 56, 60, 61, 0.1 mm; 51-55, 57-59, 0.01 mm.

vagina, slightly recurrent at its anterior extremity. The length of the vagina relative to the sizes of vestibule, sphincter and infundibulum are given in the description in this case to emphasise the extreme length of the vagina. The other features of the species are unremarkable, with cephalic papillae bearing a distal segment with an acute tip, almost equal in length to the proximal segment, eight leaf crown elements, a symmetrical buccal capsule, a slender, unornamented oesophagus, the deirid anterior to the nerve ring and the external branchlets of the dorsal ray arising after the principal bifurcation. These features together with the length of the spicules (> 3.0 mm) differentiate *C. hecale* from congeners except *C. clymene* Beveridge, 1998, *C. curta* Johnston & Mawson, 1938, *C. liebigi* Johnston & Mawson, 1938, *C. longispiculata* Johnston & Mawson, 1939, *C. nike* Beveridge, 1998, *C. robertsi* Johnston & Mawson, 1939, *C. smalesae* Mawson, 1975 and *C. solymus*. *C. hecale* is differentiated from *C. clymene* and *C. robertsi* which have six elements to the leaf crown and lip-like inflations of the peri-oral cuticle attached to each element of the leaf crown. *C. curta*, *C. liebigi*, *C. longispiculata* and *C. smalesae* all have six leaf crown elements rather than eight and the vagina is prominently recurrent in these species rather than having a short anterior recurrent section. In addition, *C. liebigi*, *C. longispiculata* and *C. smalesae* have the cervical cuticle inflated so as to form 'shoulders' in the oesophageal region. *C. nike* has submedian cephalic papillae in which the distal segment is much shorter than the proximal segment and has a sinuous vagina and a longer, slender tail in the female. *C. solymus* has a robust subcylindrical oesophagus but the submedian cephalic papillae are tiny and the anterior margin of the buccal capsule is undulate. Therefore, *C. hecale* is readily distinguishable from all known congeners.

Cloacina hyperea sp. nov.
(Figs 62–74)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31442; allotype ♀, SAM AHC 31443. Paratypes: 12♂, 8♀, SAM AHC 31444, 1♂, 1♀, BMNH 2001.4.10.7–8, 1♂, 1♀, USNPC 91136. Slide preparations of apical views of mouth and bursa, SAM AHC 28382.

Material examined: From *Dorcopsis hageni*: types.

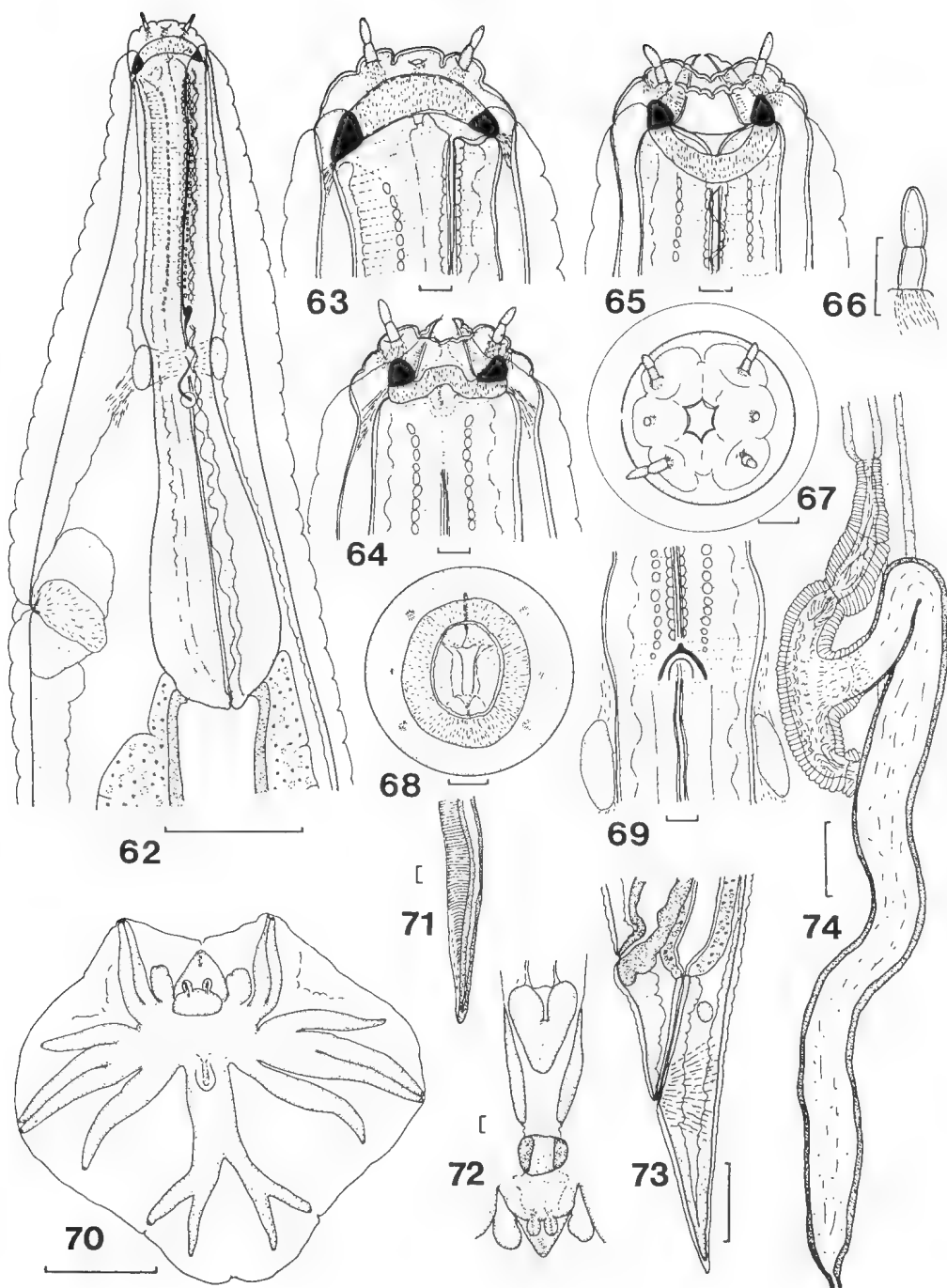
Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.034 apart. Submedian cephalic papillae prominent, 0.015 long, projecting anteriorly from peri-oral cuticle; distal segment conical, 0.007 long, only slightly shorter than cylindrical proximal segment, 0.008 long. Buccal capsule shallow, symmetrically arched anteriorly in lateral views; in dorsal views, buccal capsule arches anteriorly over dorsal oesophageal gland; in ventral views, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with prominent striations; anterior margin smooth, except on dorsal aspect. Leaf crown elements 6 in number, slightly recurved at tips; peri-oral cuticle slightly inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule. Oesophagus claviform, robust; lining with sclerotised bosses extending to level of nerve ring; single dorsal oesophageal denticle present in prominent preneural swelling. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 4.20–5.21 (4.56); maximum width 0.26–0.40 (0.34); buccal capsule 0.013–0.020 (0.016) \times 0.055–0.060 (0.056); oesophagus 0.42–0.50 (0.47); nerve ring to anterior end 0.20–0.24 (0.22); excretory pore to anterior end 0.35–0.51 (0.43); deirid to anterior end 0.25–0.34 (0.31); spicules 2.25–2.49 (2.37); gubernaculum 0.020–0.030 (0.026) long.

Dorsal ray broad at origin; major bifurcation occurs at $1/2$ length; angle of bifurcation acute; external branchlets arise after major bifurcation, as long as internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 6 specimens, types. Total length 5.25–6.14 (5.67); maximum width



FIGURES 62-74. *Cloacina hyperea* sp. nov., types. 62. Anterior end, lateral view. 63. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 64. Cephalic extremity, dorsal view. 65. Cephalic extremity, ventral view. 66. Submedian cephalic papilla, lateral view. 67. Cephalic extremity, apical view. 68. Cephalic extremity, transverse optical section through buccal capsule. 69. Preneural swelling of oesophagus, dorsal view, showing denticle. 70. Bursa, apical view. 71. Spicule tip, lateral view. 72. Gubernaculum and genital cone, dorsal view. 73. Female tail, lateral view. 74. Female genital system, lateral view. Scale bars: 62, 70, 73, 74, 0.1 mm; 63-69, 71, 72, 0.01 mm.

0.32–0.45 (0.39); buccal capsule 0.013–0.018 (0.016) x 0.058–0.060 (0.059); oesophagus 0.46–0.52 (0.49); nerve ring to anterior end 0.20–0.23 (0.22); excretory pore to anterior end 0.35–0.50 (0.45); deirid to anterior end 0.24–0.33 (0.29); tail 0.19–0.26 (0.23); vulva to posterior end 0.36–0.43 (0.39); vagina 0.96–1.24 (1.07).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg not seen.

Remarks

The anteriorly arched buccal capsule wall distinguishes *C. hyperea* sp. nov. from all congeners except *C. circe* Beveridge, 1999 and *C. laius* Beveridge, 1999, both of which occur in the quokka, *Setonix brachyurus* (Quoy & Gaimard, 1830) in the south-west of Western Australia, and from *C. nephele* sp. nov., described below. *C. hyperea* is distinguished from *C. circe* in possessing sclerotised bosses and a dorsal denticle in the oesophagus. It is differentiated from *C. laius* in having the buccal capsule less prominently arched, in having submedian cephalic papillae of a different shape, with both segments of approximately equal length, whereas in *C. laius* the proximal segment is almost twice as long as the distal segment. In addition, the spicules are 2.25–2.49 mm long in *C. hyperea* compared with 1.50–1.97 mm in *C. laius* and the vagina is commensurately longer, being 0.96–1.24 mm in *C. hyperea* compared with 0.71–0.92 mm in *C. laius*. In *C. hyperea* the internal and external branchlets of the dorsal ray are of approximately equal length whereas in *C. laius* the external branchlets are much shorter than the internal branchlets. *C. nephele* sp. nov. has lateral lips, which are absent in *C. hyperaea*, and a bulbous proximal segment to the cephalic papilla.

Cloacina nephele sp. nov. (Figs 75–89)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31445; allotype ♀, SAM AHC 31446. Paratypes: 3♂, 2♀, SAM AHC 31447, 1♂, BMNH 2001.4.10.9, 1♂, USNPC 91137. Slide preparations of apical views of mouth and bursa, SAM AHC 28384.

Material examined: From *Dorcopsis hageni*: types.

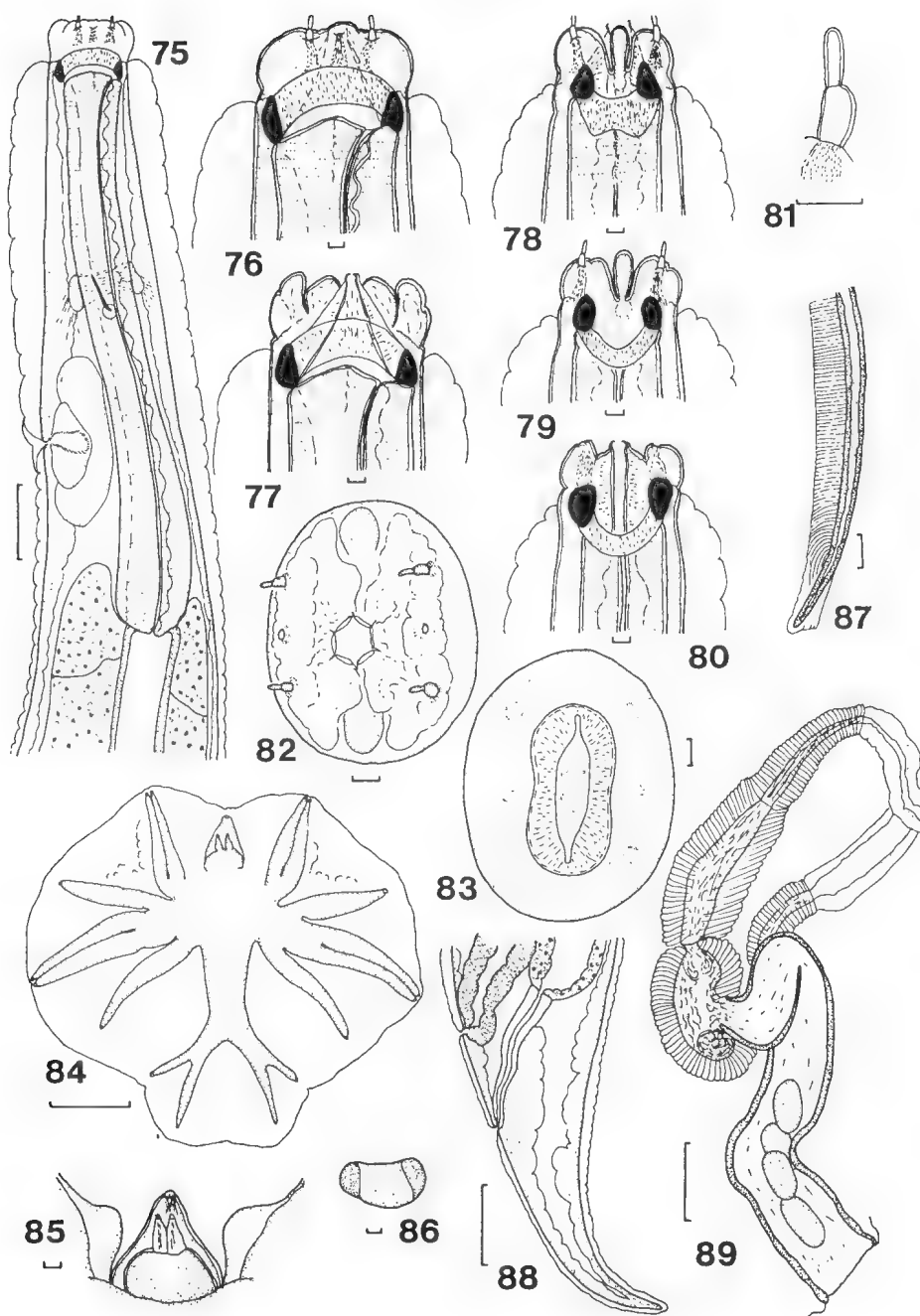
Description

Robust nematodes; cervical cuticle prominently inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.040 apart. Submedian cephalic papillae prominent, 0.020 long, projecting anteriorly from inflated peri-oral cuticle; distal segment slender, conical, 0.010 long, as long as robust, asymmetrical proximal segment, 0.010 long. Buccal capsule shallow, symmetrically arched anteriorly in lateral views; dorsally, arches anteriorly over dorsal oesophageal gland; ventrally, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with prominent striations; anterior margin smooth. Leaf crown elements 6 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element; extra dorsal and ventral projections of peri-oral cuticle present, separate from lateral arcades of amphids and submedian papillae, giving the appearance of lips. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust; lining without sclerotised bosses; denticles absent in preneural region. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 6.08–7.40 (6.66); maximum width 0.33–0.37 (0.35); buccal capsule 0.023–0.030 (0.026) x 0.090 (0.090); oesophagus 0.69–0.73 (0.71); nerve ring to anterior end 0.28–0.30 (0.29); excretory pore to anterior end 0.48–0.53 (0.51); deirid to anterior end 0.31–0.36 (0.34); spicules 1.96–2.10 (2.03); gubernaculum 0.035–0.040 (0.039) long.

Dorsal ray broad at origin, narrowing posteriorly; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 3 specimens, types. Total length 5.94–7.87 (7.02); maximum width 0.34–0.63 (0.50); buccal capsule 0.025–0.030



FIGURES 75–89. *Cloacina nephele* sp. nov., types. 75. Anterior end, lateral view. 76. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 77. Cephalic extremity, lateral view, dorsal aspect on right-hand side, median optical section showing leaf crown elements and inflation of cephalic collar. 78. Cephalic extremity, dorsal view. 79. Cephalic extremity, ventral view. 80. Cephalic extremity, ventral view, median optical section showing leaf crown elements. 81. Submedian cephalic papilla, lateral view. 82. Cephalic extremity, apical view. 83. Cephalic extremity, transverse optical section through buccal capsule. 84. Bursa, apical view. 85. Genital cone, dorsal view. 86. Gubernaculum, ventral view. 87. Spicule tip, lateral view. 88. Female tail, lateral view. 89. Female genital system, lateral view. Scale bars: 75, 84, 88, 89, 0.1 mm; 76–83, 85–87, 0.01 mm.

(0.027) x 0.100 (0.100); oesophagus 0.72–0.79 (0.76); nerve ring to anterior end 0.29–0.32 (0.30); excretory pore to anterior end 0.46–0.58 (0.52); deirid to anterior end 0.30–0.31 (0.31); tail 0.31–0.39 (0.35); vulva to posterior end 0.43–0.55 (0.48); vagina 0.51–0.66 (0.59); egg 0.080–0.085 (0.083) x 0.040–0.045 (0.043).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

C. nephele sp. nov. closely resembles *C. circe*, *C. laius* and *C. hyperea* in having an anteriorly arched buccal capsule. It differs from *C. laius* and *C. hyperea* in lacking oesophageal bosses and denticles, and differs from *C. circe* in having a markedly inflated cervical cuticle, cephalic papillae in which the distal segment is not oriented medially, and a recurrent vagina. It differs from all of these species in having a swollen cephalic collar and lip-like inflations of the peri-oral cuticle attached to each leaf crown element. The dorsal and ventral 'lips' are unique within the genus.

Cloacina oweni sp. nov. (Figs 90–101)

Synonyms: *Cloacina* sp. nov. of Beveridge, 1998, p. 506 (*Macropus agilis*).

Types: From stomach of *Macropus agilis*, Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998. Holotype ♂, SAM AHC 31448; allotype ♀, SAM AHC 31449. Paratypes: 51♂, 55♀, SAM AHC 31450, 1♂, 1♀, BMNH 1998.9.28.11–12.

Material examined: From *Macropus agilis*: types; 1♂, 1♀, Dari, Bensbach, Papua New Guinea, SAM AHC 11719.

Description

Robust nematodes; cervical cuticle slightly inflated to level of excretory pore; transverse cuticular annulations widely spaced, 0.030 apart. Submedian cephalic papillae prominent, 0.013 long, projecting anteriorly from inflated peri-oral cuticle; distal segment ovoid, 0.004 long, shorter than cylindrical proximal segment, 0.008 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; octagonal in transverse section, wider than deep, wall without prominent striations; anterior margin smooth. Leaf crown

elements 8 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust; lining without sclerotised bosses; single dorsal denticle present at level of nerve ring; preneural swelling absent. Nerve ring in mid-oesophageal region; deirids in anterior oesophageal region; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 10 specimens, types. Total length 5.48–7.50 (6.73); maximum width 0.26–0.43 (0.34); buccal capsule 0.015–0.025 (0.019) x 0.045–0.070 (0.056); oesophagus 0.53–0.65 (0.60); nerve ring to anterior end 0.25–0.32 (0.27); excretory pore to anterior end 0.26–0.53 (0.44); deirid to anterior end 0.10–0.16 (0.12); spicules 2.19–2.67 (2.46); gubernaculum 0.025–0.040 (0.031) long.

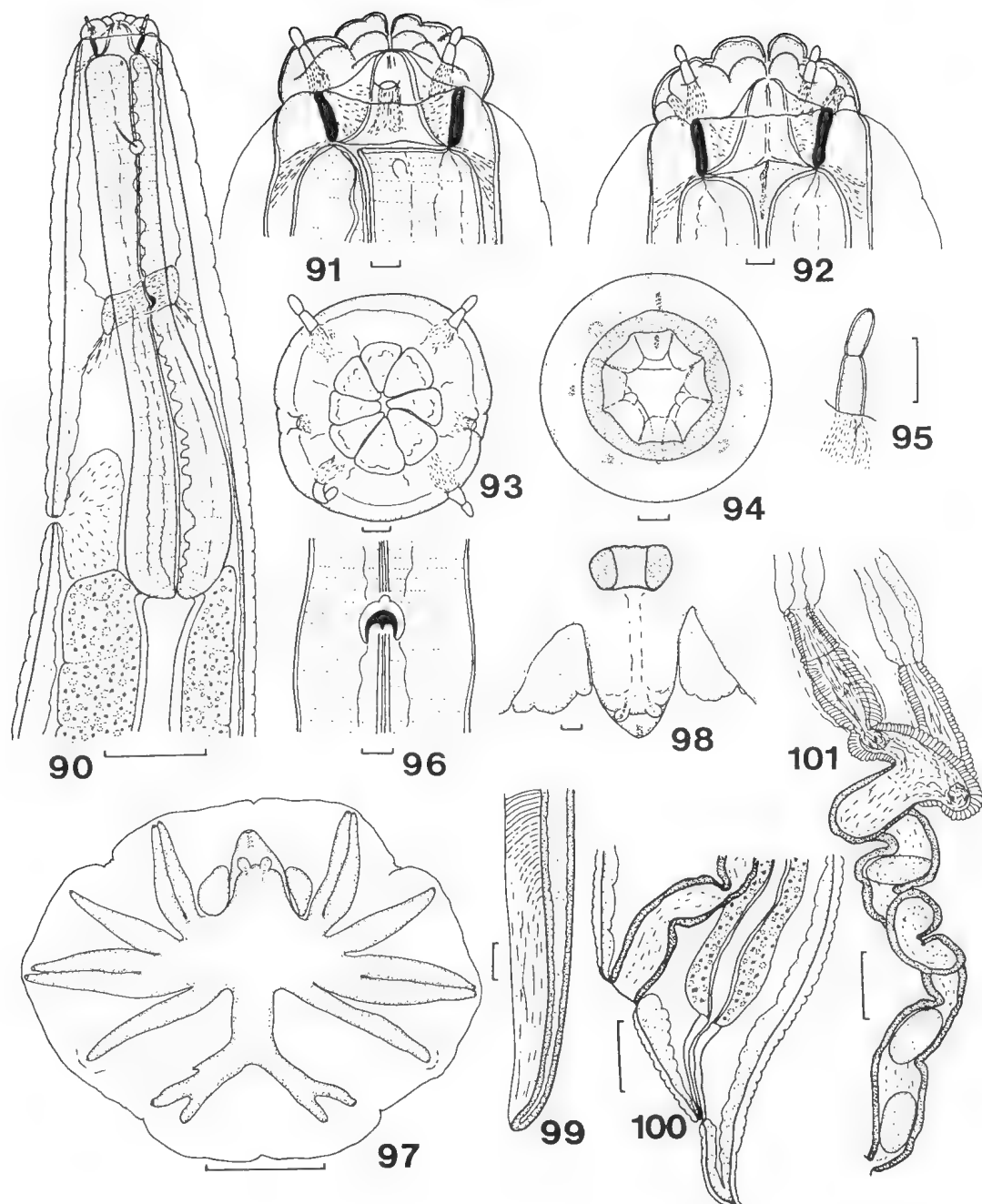
Dorsal ray broad at origin; major bifurcation occurs at 1/3 length; angle of bifurcation obtuse; external branchlets arise after major bifurcation, near extremity of ray, slightly longer and more robust than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt, slightly recurved; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 6.70–9.36 (8.06); maximum width 0.30–0.61 (0.46); buccal capsule 0.015–0.025 (0.020) x 0.045–0.075 (0.057); oesophagus 0.55–0.76 (0.64); nerve ring to anterior end 0.24–0.33 (0.28); excretory pore to anterior end 0.32–0.61 (0.48); deirid to anterior end 0.09–0.16 (0.11); tail 0.14–0.21 (0.17); vulva to posterior end 0.27–0.34 (0.31); vagina 0.45–0.70 (0.58); egg 0.090–0.100 (0.093) x 0.040–0.050 (0.048).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, convoluted, not recurrent; egg ellipsoidal.

Remarks

The prominent lips and symmetrical buccal capsule distinguish *C. oweni* sp. nov. from all congeners except *C. artemis* Beveridge, 1998, *C. caenis* Beveridge, 1998, *C. clymene*, *C. dindymene* Beveridge, 1998, *C. hypsipyle*, *C.*



FIGURES 90–101. *Cloacina oweni* sp. nov., types. 90. Anterior end, lateral view. 91. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 92. Cephalic extremity, dorsal view. 93. Cephalic extremity, apical view. 94. Cephalic extremity, transverse optical section through buccal capsule. 95. Submedian cephalic papilla, lateral view. 96. Preneural region of oesophagus, showing denticle, dorsal view. 97. Bursa, apical view. 98. Genital cone, dorsal view and gubernaculum. 99. Spicule tip, lateral view. 100. Female tail, lateral view. 101. Female genital system, lateral view. Scale bars: 90, 97, 100, 101, 0.1 mm; 91–96, 98, 99, 0.01 mm.

linstowi Johnston & Mawson, 1940, *C. maia* Beveridge, 1998, *C. parva*, *C. robertsi*, *C. smalesae*, *C. thetidis* Johnston & Mawson, 1939 and *C. wallabiae* Johnston & Mawson, 1939. The presence of a single dorsal denticle in the oesophagus and the lack of oesophageal bosses distinguishes it from all of these species except *C. dindymene*. It differs from *C. dindymene* in the shape of the submedian cephalic papillae which have elongated distal segments in *C. dindymene*, and in the shape of the dorsal ray, the bifurcations of which form an acute angle in *C. dindymene* rather than the obtuse angle seen in *C. oweni*. In features of the head, *C. oweni* is most likely to be confused with *C. robertsi*, found in rock wallabies of the genus *Petrogale* Gray, 1837 in eastern Australia. *C. oweni* is readily differentiated, however, by the oesophageal denticle and the lack of a prominently recurrent vagina as exhibited by *C. robertsi*.

C. oweni is abundant in the stomachs of agile wallabies in the Bula Plain region of Papua New Guinea, but has not been found in the same host species in northern Australia in spite of relatively intensive examination of this host in all of the northern states (Speare et al. 1983; Beveridge et al. 1998). More surprising is the close resemblance of this species to congeners occurring in rock wallabies in Australia, a relationship for which no simple explanation currently exists.

***Cloacina papuensis* sp. nov.**
(Figs 102–115)

Types: From stomach of *Macropus agilis*, Bula Plain, Bensbach, Papua New Guinea, coll. I. Owen, May, 1998. Holotype ♂, SAM AHC 31451; allotype ♀, SAM AHC 31452. Paratypes: 5♂, 6♀, SAM AHC 31453, 1♂, 1♀, BMNH 1998.9.28.13–14. Slide preparations of apical view of mouth and bursa, SAM AHC 28386.

Material examined: From *Macropus agilis*: types.

Description

Small nematodes; cervical cuticle not inflated; transverse cuticular annulations widely spaced, 0.010 apart. Submedian cephalic papillae small, conical, 0.006 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.002 long, shorter than cylindrical proximal segment, 0.004 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; circular in

transverse section, wider than deep, wall without prominent striations; anterior margin smooth. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle not inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland in prominent, bilobed, tooth-like structure projecting into lumen of buccal capsule; each ventral sector with 2 triangular sclerotised projections. Oesophagus claviform, slender; lining without sclerotised bosses; single dorsal denticle present immediately anterior to nerve ring; preneural swelling present. Nerve ring in mid-oesophageal region; deirids in anterior oesophageal region; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 5 specimens, types. Total length 3.18–5.09 (4.57); maximum width 0.18–0.32 (0.23); buccal capsule 0.007–0.010 (0.008) x 0.020–0.026 (0.021); oesophagus 0.31–0.41 (0.36); nerve ring to anterior end 0.16–0.17 (0.17); excretory pore to anterior end 0.20–0.34 (0.28); deirid to anterior end 0.08–0.11 (0.10); spicules 1.84–2.26 (2.05); gubernaculum 0.025–0.030 (0.029) long.

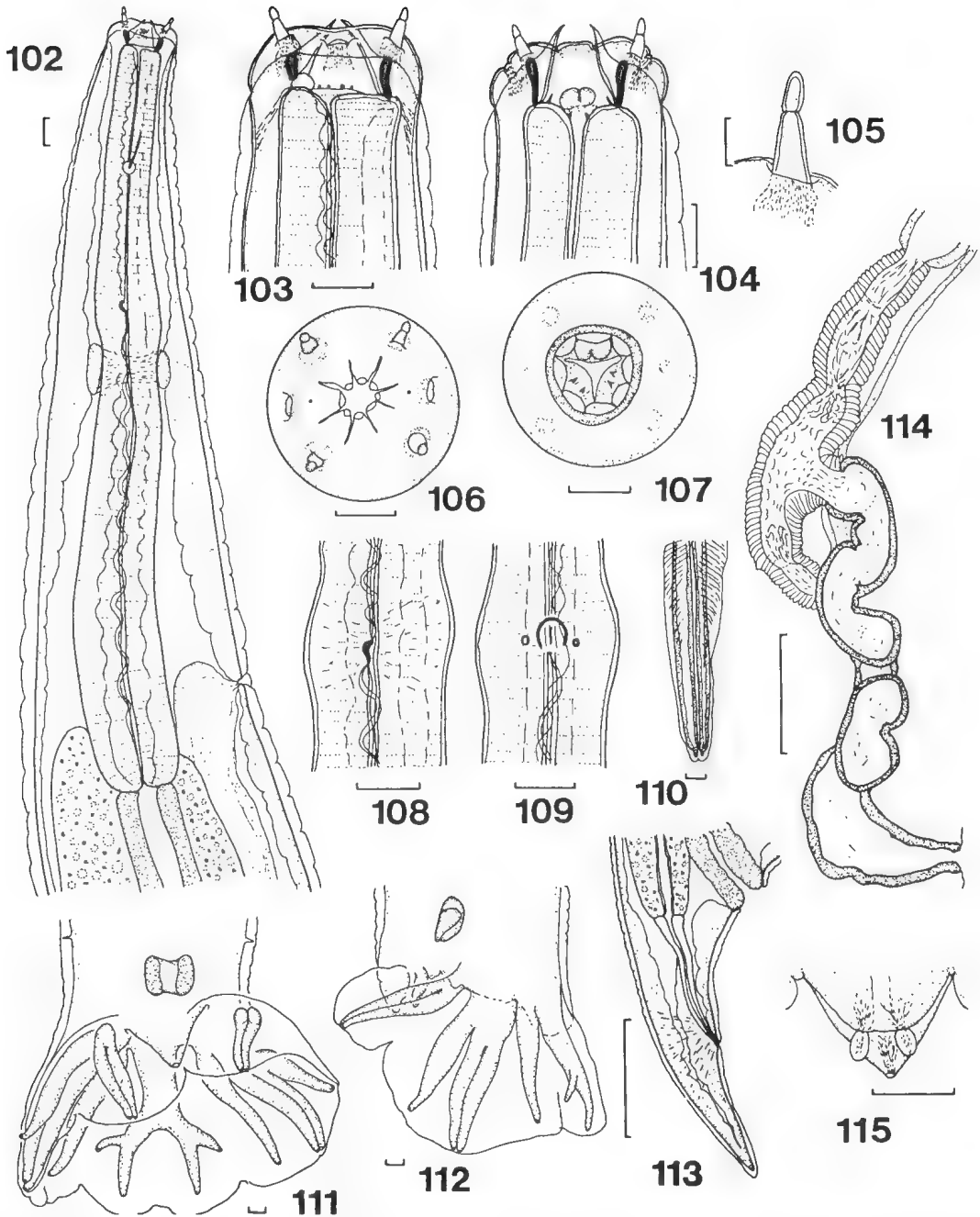
Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, shorter and more robust than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip bifid; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 5.14–6.05 (5.57); maximum width 0.25–0.36 (0.32); buccal capsule 0.005–0.008 (0.007) x 0.020–0.025 (0.023); oesophagus 0.35–0.39 (0.38); nerve ring to anterior end 0.17–0.18 (0.17); excretory pore to anterior end 0.23–0.38 (0.33); deirid to anterior end 0.07–0.011 (0.09); tail 0.14–0.22 (0.19); vulva to posterior end 0.30–0.44 (0.39); vagina 0.47–0.63 (0.53); egg 0.070–0.085 (0.080) x 0.040–0.050 (0.046).

Female tail short, conical; vulva immediately anterior to anus; vagina elongate, convoluted, not recurrent; egg ellipsoidal.

Remarks

The simple, symmetrical buccal capsule, lack of



FIGURES 102–115. *Cloacina papuensis* sp. nov., types. 102. Anterior end, lateral view. 103. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 104. Cephalic extremity, dorsal view. 105. Submedian cephalic papilla, lateral view. 106. Cephalic extremity, apical view. 107. Cephalic extremity, transverse optical section through buccal capsule. 108. Preneural region of oesophagus, showing denticle, lateral view, dorsal aspect on left-hand side. 109. Preneural region of oesophagus, showing denticle, dorsal view. 110. Spicule tips, ventral view. 111. Bursa, ventral view. 112. Bursa, lateral view. 113. Female tail, lateral view. 114. Female genital system, lateral view. 115. Genital cone, dorsal view. Scale bars: 113, 114, 0.1 mm; 102–104, 106–112, 115 0.01 mm; 105, 0.003 mm.

prominent lips and unornamented oesophagus with a single dorsal denticle differentiate *C. papuensis* sp. nov. from all congeners except *C. cornuta*, *C. dirce*, *C. longispiculata* and *C. sciron*. *C. papuensis* is differentiated from *C. sciron* primarily in having the deirid anterior to, rather than at the level of, the nerve ring. In *C. sciron*, the anterior margin of the buccal capsule arches anteriorly and is sinuous. *C. papuensis* differs from *C. longispiculata* in lacking the prominent shoulder-like inflations of the cervical cuticle, in having the excretory pore at the level of the oesophago-intestinal junction rather than well posterior to it as in *C. longispiculata*, and in having eight leaf crown elements rather than the six present in *C. longispiculata*. It differs from *C. dirce* in lacking the prominent cervical inflation of the cuticle, in the shape of the submedian papillae which have an extended distal segment in *C. dirce*, in spicule lengths (1.84–2.26 (2.05) mm long in *C. papuensis*, 3.48–3.95 (3.70) mm long in *C. dirce*), and in the shape of the vagina which is longer and more convoluted in *C. dirce*. Therefore, *C. papuensis* most closely resembles *C. cornuta*, also a parasite of *Macropus agilis*, in having a prominent dorsal oesophageal tooth. It differs from *C. cornuta* in lacking a cervical cuticular inflation, in the shape of the submedian papillae which have elongate distal segments in *C. cornuta*, in the shape of the dorsal ray which in *C. cornuta* terminates in very short subequal internal and external branchlets, in spicule length (1.84–2.26 (2.05) in *C. papuensis*, 1.38–1.62 (1.51) mm in *C. cornuta*), and in the length and shape of the female tail which is very short and prominently swollen in *C. cornuta*.

***Cloacina polymela* sp. nov.**
(Figs 116–128)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31454; allotype ♀, SAM AHC 31455. Paratypes: 4♂, 8♀, SAM AHC 31456, 1♂, 1♀, BMNH 2001.4.10.10–11, 1♂, 1♀, USNPC 91138. Slide preparations of apical views of mouth and bursa, SAM AHC 28387.

Material examined: From *Dorcopsis hageni*: types.

Description

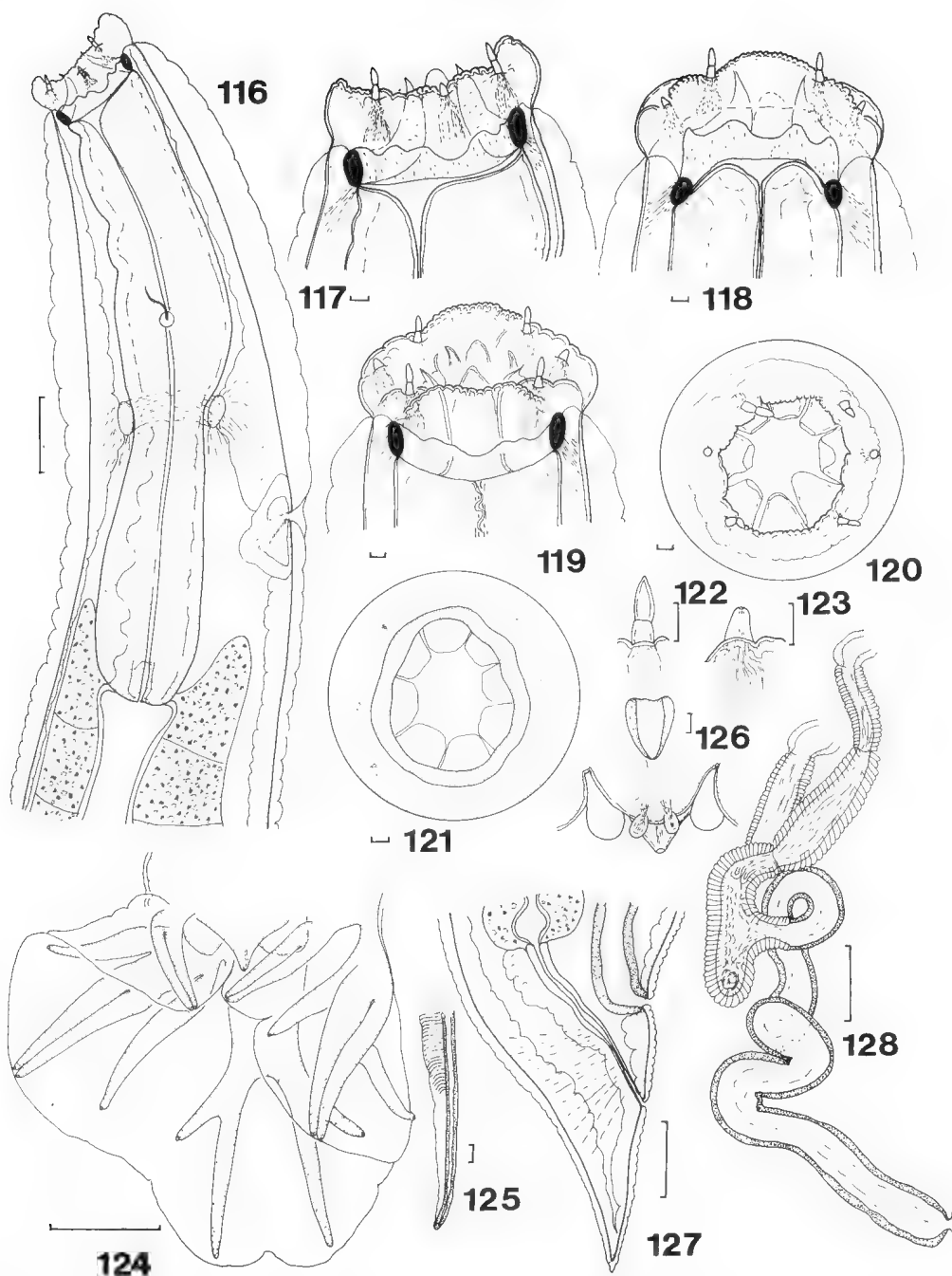
Robust nematodes; anterior extremity deviated dorsally; cervical cuticle inflated to level of

excretory pore; transverse cuticular annulations widely spaced, 0.030–0.062 apart. Submedian cephalic papillae prominent, 0.016 long, projecting anteriorly from inflated peri-oral cuticle; distal segment acute, conical, 0.010 long, longer than cylindrical proximal segment, 0.006 long. Cephalic collar prominently inflated on dorsal and ventral aspects, anterior margin of collar rugose; amphids conical, projecting above level of cephalic collar. Buccal capsule very shallow, symmetrical, anterior margin highly sinuous; due to dorsal deviation of anterior extremity, buccal capsule appears to arch dorsally in ventral views; oval and dorso-ventrally elongate in transverse section, wider than deep, wall finely striated. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, robust, anterior section of greater diameter than region posterior to nerve ring; lining without sclerotised bosses; denticles absent in preneural region. Nerve ring posterior to mid point of oesophagus; deirids slightly anterior to level of nerve ring; excretory pore between nerve ring and oesophago-intestinal junction.

Male. Measurements of 9 specimens, types. Total length 5.86–6.03 (5.93); maximum width 0.29–0.46 (0.39); buccal capsule 0.020–0.030 (0.025) x 0.115–0.150 (0.130); oesophagus 0.66–0.79 (0.72); nerve ring to anterior end 0.44–0.53 (0.48); excretory pore to anterior end 0.55–0.70 (0.65); deirid to anterior end 0.36–0.45 (0.39); spicules 2.61–2.71 (2.65); gubernaculum 0.035–0.050 (0.045) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise after major bifurcation, much shorter than internals, directed posterolaterally, not reaching margin of bursa; internal branchlets elongate, directed posteriorly, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, subcordate. Spicule tip blunt, slightly recurved; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Measurements of 10 specimens, types. Total length 5.45–8.22 (7.14); maximum width 0.33–0.59 (0.46); buccal capsule 0.015–0.030 (0.025) x 0.120–0.160 (0.150); oesophagus 0.70–



FIGURES 116–128. *Cloacina polymela* sp. nov., types. 116. Anterior end, lateral view, showing dorsal deviation of head. 117. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 118. Cephalic extremity, ventral view. 119. Cephalic extremity, dorsal view. 120. Cephalic extremity, apical view. 121. Cephalic extremity, transverse optical section through buccal capsule. 122. Submedian cephalic papilla, lateral view. 123. Amphid, lateral view. 124. Bursa, ventral view. 125. Spicule tip, ventral view. 126. Gubernaculum and genital cone, dorsal view. 127. Female tail, lateral view. 128. Female genital system, lateral view. Scale bars: 116, 124, 127, 128, 0.1 mm; 117–123, 125, 126, 0.01 mm.

0.94 (0.82); nerve ring to anterior end 0.45–0.61 (0.54); excretory pore to anterior end 0.55–0.85 (0.75); deirid to anterior end 0.31–0.50 (0.42); tail 0.21–0.30 (0.24); vulva to posterior end 0.33–0.50 (0.38); vagina 0.49–0.68 (0.60); egg 0.080–0.085 (0.082) x 0.040–0.045 (0.042).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina polymela sp. nov. is a highly distinctive species which differs from all congeners in having the anterior extremity deviated dorsally. This feature appears in every specimen and therefore is not likely to be a fixation artefact. In addition, it differs from congeners except *C. dryope* Beveridge, 1998 and *C. sappho* in having an oesophagus in which the preneural region is of greater diameter than the posterior part. *C. polymela* is distinguished from *C. dryope* in having eight rather than six leaf crown elements; in having a more posterior deirid, in having the excretory pore anterior to the oesophago-intestinal junction rather than posterior to it, and in the shape of the buccal capsule which is extremely shallow in *C. dryope* and in which the anterior margin has only slight saliences rather than prominent undulations. *C. polymela* and *C. sappho* are the only two members of the genus in which the amphids form acutely pointed conical projections above the cephalic collar. In all other species, the amphids are dome-shaped and do not project obviously beyond the collar. *C. polymela* also resembles *C. sappho* in the shape of the dorsal ray of the bursa and in possessing eight leaf crown elements. However, it differs in having prominent inflations of the cephalic collar on the dorsal and ventral surface, a feature which resembles the lip-like projections present in *C. nephele*. *C. polymela* also differs from *C. sappho* in spicule length (2.61–2.71 (2.65) mm in *C. polymela*; 1.30–1.50 (1.38) mm in *C. sappho*) and in the shape of the vagina which is recurrent in *C. polymela* but short and straight in *C. sappho*.

Cloacina praxitheia sp. nov. (Figs 129–138)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31457. Paratypes: 2♂, SAM AHC 31458, 1♂,

BMNH 2001.4.10.12; 1♂, USNPC 91139. Slide preparations of apical views of mouth and bursa, SAM AHC 28388.

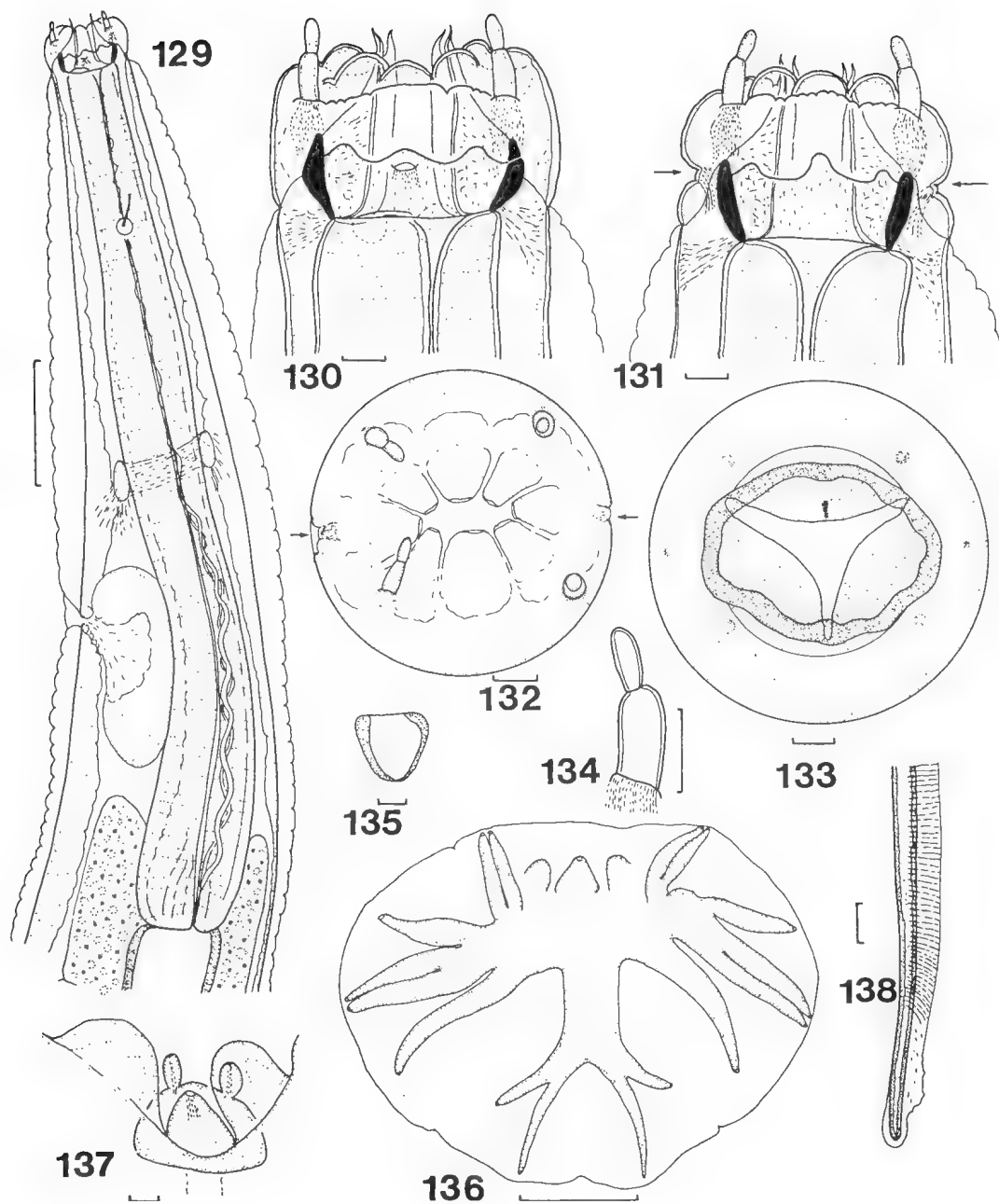
Material examined: From *Dorcopsis hageni*: types.

Description

Robust nematodes; cervical cuticle slightly inflated to beyond level of excretory pore; transverse cuticular annulations widely spaced, 0.015 apart. Submedian cephalic papillae prominent, 0.019 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.008 long, deviated medially, slightly shorter than asymmetrical, cylindrical proximal segment, 0.011 long; submedian papillae situated anteriorly on cephalic collar; amphids situated posteriorly, below anterior margin of buccal capsule in lateral views. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views, wall with faint striations; anterior margin undulate, with anterior projections associated with each leaf crown element. Leaf crown elements 8 in number, not recurved at tips; peri-oral cuticle inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus subcylindrical, almost claviform at base, robust; lining without sclerotised bosses or denticles; preneural swelling of oesophagus absent. Nerve ring in mid-oesophageal region; deirids anterior to nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 6 specimens, types. Total length 3.71–5.34 (4.86); maximum width 0.32–0.38 (0.36); buccal capsule 0.015–0.018 (0.016) x 0.050–0.055 (0.054); oesophagus 0.66–0.78 (0.71); nerve ring to anterior end 0.34–0.38 (0.36); excretory pore to anterior end 0.43–0.49 (0.46); deirid to anterior end 0.27–0.32 (0.30); spicules 1.30–1.58 (1.43); gubernaculum 0.030–0.040 (0.033) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise immediately after major bifurcation, much shorter than internals, directed postero-laterally, not reaching margin of bursa; internal branchlets directed posteriorly, not reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, subcordate, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width then terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior



FIGURES 129–138. *Cloacina praxithea* sp. nov., types. 129. Anterior end, lateral view. 130. Cephalic extremity, lateral view, dorsal aspect on right-hand side. 131. Cephalic extremity, dorsal view; arrows indicate amphids. 132. Cephalic extremity, apical view; arrows indicate amphids. 133. Cephalic extremity, transverse optical section through buccal capsule. 134. Submedian cephalic papilla, lateral view. 135. Gubernaculum, ventral view. 136. Bursa, apical view. 137. Genital cone, dorsal view. 138. Spicule tip, lateral view. Scale bars: 129, 136, 0.1 mm; 130–135, 137, 138, 0.01 mm.

lip with paired projections and cuticular inflation of internal surface of bursa on either side.

Female. Not seen

Remarks

Cloacina praxithea sp. nov. is distinguished from all congeners by the position of the amphids on the cephalic collar. In other species the amphids are at the same level as the submedian papillae, anterior to the level of the buccal capsule, while in *C. praxithea* the amphids, in lateral view, are below the level of the anterior margin of the buccal capsule (Fig. 130). *C. praxithea* is characterised by a symmetrical, lobed buccal capsule without bosses or denticles in the oesophagus. As such, it has similarities with the Australian species *C. artemis*, *C. dryope*, *C. hebe*, *C. hypsipyle*, *C. linstowi*, *C. maia*, *C. thetidis* and *C. wallabiae*, all of which differ from it in having six rather than eight leaf crown elements. Among the species known from New Guinea, the features of the buccal capsule, as well as the presence of eight leaf crown elements, indicate affinities with *C. syphax*, *C. solon*, *C. sappho* and *C. solymus*. *C. solymus* has tiny cephalic papillae, in striking contrast to the prominent papillae of *C. praxithea*, while *C. sappho* and *C. polymela* have the amphids on or forming projections beyond the level of the cephalic collar; *C. solon* has a greatly inflated cervical cuticle and its spicules are 2.60–2.95 (2.81) mm in length compared with 1.93–2.05 (1.99) mm in *C. praxithea*; *C. syphax* differs in having the lateral branchlets of the dorsal ray arise anterior to the principal bifurcation. Therefore, *C. praxithea* is readily distinguishable from all congeners even in the absence of females, which are currently unknown.

Cloacina procris sp. nov.
(Figs 139–153)

Types: From stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987. Holotype ♂, SAM AHC 31459; allotype ♀, SAM AHC 31460. Paratypes: 1♂, 2♀, SAM AHC 31461. Slide preparations of apical views of mouth and bursa, SAM AHC 28389.

Material examined: From *Dorcopsis hageni*: types.

Description

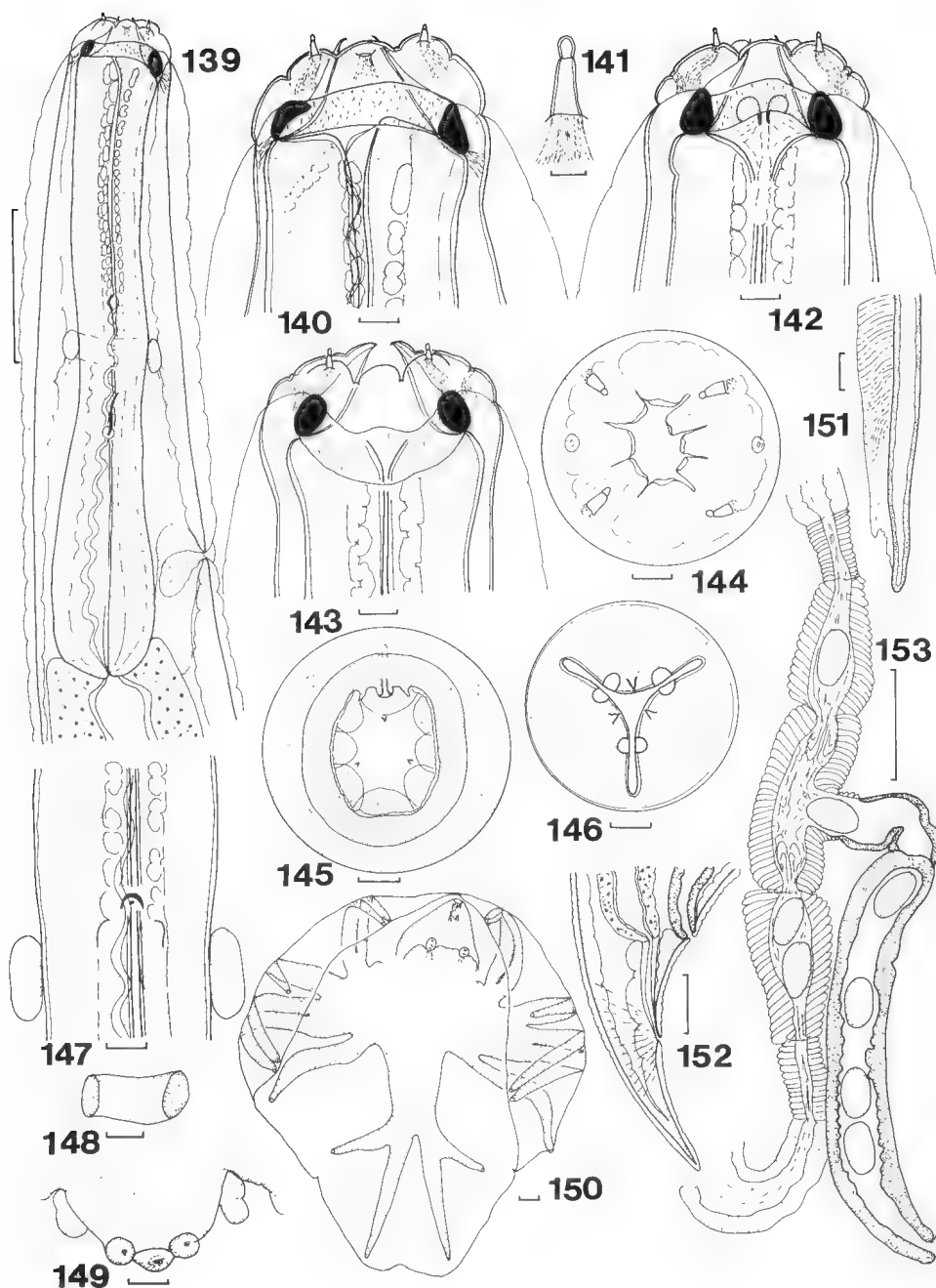
Robust nematodes; cervical cuticle slightly inflated to level of excretory pore; transverse

cuticular annulations widely spaced, 0.020 apart. Submedian cephalic papillae small, 0.0035 long, projecting anteriorly from peri-oral cuticle; distal segment ovoid, 0.0005 long, much shorter than cylindrical proximal segment, 0.003 long. Buccal capsule shallow, asymmetrical in lateral views, deeper on ventral side, slight anterior arching of capsule; dorsally, capsule arches anteriorly over dorsal oesophageal tooth; ventrally, curves posteriorly; oval and dorso-ventrally elongate in transverse section, wider than deep, wall with faint striations; anterior margin smooth. Leaf crown elements 8 in number, not recurved at tips; peri-oral cuticle very slightly inflated into lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, projecting prominently into lumen of buccal capsule; each sector of oesophagus bears single triangular tooth-like structure projecting into lumen. Oesophagus claviform, robust; lining with sclerotised bosses extending to level of nerve ring; single dorsal oesophageal denticle present in preneural region; preneural swelling of oesophagus absent. Nerve ring in mid-oesophageal region; deirids posterior to nerve ring; excretory pore at level of, or slightly anterior to, oesophago-intestinal junction.

Male. Measurements of 3 specimens, types. Total length 3.25–4.52 (3.89); maximum width 0.17–0.32 (0.26); buccal capsule 0.015–0.018 (0.017) x 0.050–0.060 (0.054); oesophagus 0.40–0.41 (0.40); nerve ring to anterior end 0.20–0.21 (0.21); excretory pore to anterior end 0.35–0.40 (0.38); deirid to anterior end 0.27–0.32 (0.30); spicules 1.30–1.58 (1.43); gubernaculum 0.030 (0.030) long.

Dorsal lobe of bursa elongate; dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation acute; external branchlets arise at level of major bifurcation, much shorter than internals, directed almost laterally, not reaching margin of bursa; internal branchlets directed posteriorly, reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip blunt; ala diminishes gradually in width then terminates abruptly anterior to spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflations of internal surface of bursa on either side.

Female. Measurements of 3 specimens, types. Total length 4.26–5.15 (4.64); maximum width 0.37–0.47 (0.42); buccal capsule 0.018–0.020 (0.019) x 0.060–0.065 (0.062); oesophagus



FIGURES 139–153. *Cloacina procris* sp. nov., types. 139. Anterior end, lateral view. 140. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 141. Submedian cephalic papilla, lateral view. 142. Cephalic extremity, dorsal view. 143. Cephalic extremity, ventral view. 144. Cephalic extremity, apical view. 145. Cephalic extremity, transverse optical section through buccal capsule. 146. Transverse optical section through anterior extremity of oesophagus showing bosses and three tooth-like projections in each of the oesophageal sectors. 147. Preneural region of oesophagus, dorsal view, showing denticle. 148. Gubernaculum, ventral view. 149. Genital cone, dorsal view. 150. Bursa, apical view. 151. Spicule tip, lateral view. 152. Female tail, lateral view. 153. Female genital system, lateral view. Scale bars: 139, 152, 153, 0.1 mm; 140, 142–151, 0.01 mm; 141, 2.5 µm.

0.48–0.50 (0.49); nerve ring to anterior end 0.21–0.22 (0.22); excretory pore to anterior end 0.36–0.40 (0.38); deirid to anterior end 0.29–0.33 (0.31); tail 0.19–0.27 (0.23); vulva to posterior end 0.35–0.47 (0.40); vagina 0.52–0.60 (0.53); egg 0.050–0.060 (0.055) x 0.030–0.035 (0.032).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, straight, turns abruptly at entry to vestibule; egg ellipsoidal.

Remarks

Although described from only a small series of specimens, *C. procris* sp. nov. is quite distinctive morphologically. It is characterised by very small submedian cephalic papillae, a slightly asymmetrical, arched buccal capsule, eight leaf crown elements, bosses lining the anterior region of the oesophagus, a single, small oesophageal denticle, deirid posterior to the nerve ring, an elongate dorsal ray with the external branchlets arising immediately after the principal bifurcation, and a straight vagina. These features distinguish the species from all congeners.

The asymmetrical buccal capsule, oesophageal bosses and dorsal denticle with the posterior position of the deirid distinguish the species from all others except *C. eos* Beveridge, 1998, *C. papillata* Beveridge, 1979 and *C. sterope*. In *C. eos* and *C. papillata* there are only six rather than eight leaf crown elements and the vagina is prominently recurrent. In *C. sterope*, the buccal capsule exhibits a much greater degree of asymmetry, the submedian cephalic papillae are larger and more prominent and the spicules are longer (1.67–2.07 (1.96) mm in *C. sterope*, 1.30–1.58 (1.43) mm in *C. procris*).

Cloacina sterope Beveridge & Speare, 1999

Material examined: 3♂, 4♀, from stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987, SAM AHC 31462.

Remarks

Cloacina sterope was described by Beveridge and Speare (1999) from *Dorcopsulus vanheurni* from the Chimbu Province of New Guinea. Morphological features as well as measurements of the new specimens from *D. hageni* agree well with the original description. *D. hageni* represents a new host record.

Cloacina syphax Beveridge & Speare, 1999

Material examined: 17♂, 9♀, from stomach of *Dorcopsis hageni*, Usino, Madang, Papua New Guinea, coll. T. Reardon, May, 1987, SAM AHC 31469; BMNH 2001.4.10.13.

Remarks

Cloacina syphax was described from *Dorcopsulus vanheurni* by Beveridge and Speare (1999). The current collection represents a new host record.

Cloacina theope sp. nov.

(Figs 154–166)

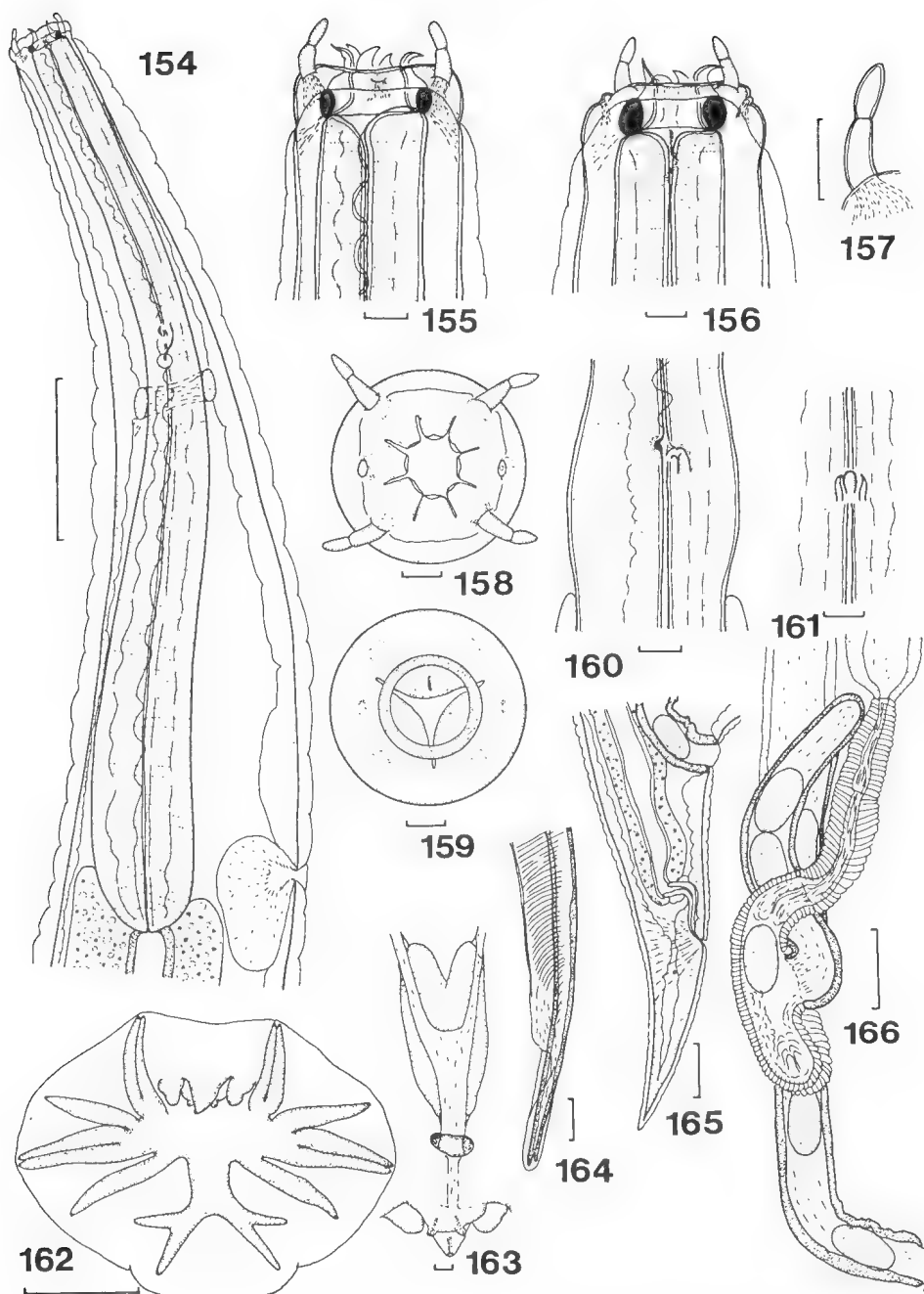
Types: From stomach of *Dendrolagus matschiei* Forster & Rothschild, 1907, Huon Peninsula, Morobe Province, Papua New Guinea, coll. J. Mayer, July 1999. Holotype ♂, USNPC 91140; allotype ♀, USNPC 91141. Paratypes: 2♂, 4♀, USNPC 91142; 1♂, on slides, SAM AHC 28390.

Material examined: From *Dendrolagus matschiei*: types. From *Dendrolagus dorianus*: 10♂, 5♀, Lake Trist, Papua New Guinea, coll. I. Redmond, 1979, BMNH 1981. 4486–4505.

Description

Robust nematodes; cervical cuticle slightly inflated; transverse cuticular annulations widely spaced, 0.021–0.044 apart. Submedian cephalic papillae prominent, 0.017 long, projecting anteriorly from inflated peri-oral cuticle; distal segment ovoid, 0.008 long, directed slightly medially, slightly shorter than robust, asymmetrical proximal segment, 0.009 long. Buccal capsule shallow, symmetrical in lateral and dorso-ventral views; circular in transverse section, wall without prominent striations; anterior margin smooth. Leaf crown elements 8 in number, recurved at tips; peri-oral cuticle not inflated into lip-like lobes attached to each element. Dorsal sector of oesophagus bearing opening of dorsal oesophageal gland, not projecting into lumen of buccal capsule. Oesophagus claviform, slender; lining without sclerotised bosses; denticles present in preneural region; dorsal denticle prominent; two subventral thickenings of oesophageal lining giving appearance of denticles, at same level as dorsal denticle. Nerve ring in mid-oesophageal region; deirids at level of nerve ring; excretory pore at level of oesophago-intestinal junction.

Male. Measurements of 4 specimens, types. Total length 4.68–5.04 (4.88); maximum width



FIGURES 154–166. *Cloacina theope* sp. nov., types. 154. Anterior end, lateral view. 155. Cephalic extremity, lateral view, dorsal aspect on left-hand side. 156. Cephalic extremity, dorsal view. 157. Submedian cephalic papilla, lateral view. 158. Cephalic extremity, apical view. 159. Cephalic extremity, transverse optical section through buccal capsule. 160. Preneural region of oesophagus, lateral view, dorsal aspect on left-hand side, showing denticles. 161. Preneural region of oesophagus, dorsal view, showing denticles. 162. Bursa, apical view. 163. Gubernaculum, genital cone and spicule sheaths, dorsal view. 164. Spicule tip, lateral view. 165. Female tail, lateral view. 166. Female genital system, lateral view. Scale bars: 154, 162, 165, 166, 0.1 mm; 155–161, 163–164, 0.01 mm.

0.30–0.32 (0.31); buccal capsule 0.010 (0.010) x 0.030–0.033 (0.031); oesophagus 0.51–0.60 (0.55); nerve ring to anterior end 0.18–0.20 (0.19); excretory pore to anterior end 0.31–0.41 (0.35); deirid to anterior end 0.13–0.23 (0.18); spicules 2.29–2.63 (2.52); gubernaculum 0.015–0.020 (0.018) long.

Dorsal ray broad at origin; major bifurcation occurs at 1/2 length; angle of bifurcation obtuse; external branchlets arise immediately after major bifurcation, shorter than internals, directed laterally, not reaching margin of bursa; internal branchlets directed postero-laterally, almost reaching margin of bursa. Externo-dorsal ray not reaching margin of bursa. Gubernaculum prominent, slightly wider than long. Spicule tip minutely bifid; ala diminishes gradually in width towards spicule tip; anterior lip of genital cone conical; posterior lip with paired projections and cuticular inflations of internal surface of bursa on either side.

Female. Measurements of 5 specimens, types. Total length 6.09–6.71 (6.29); maximum width 0.39–0.43 (0.41); buccal capsule 0.008–0.010 (0.009) x 0.030–0.035 (0.032); oesophagus 0.52–0.64 (0.59); nerve ring to anterior end 0.25 (0.25); excretory pore to anterior end 0.30–0.51 (0.43); deirid to anterior end 0.14–0.23 (0.20); tail 0.28–0.36 (0.33); vulva to posterior end 0.49–0.68 (0.59); vagina 1.03–1.33 (1.19); egg 0.085–0.095 (0.089) x 0.045–0.050 (0.048).

Female tail slender, conical; vulva immediately anterior to anus; vagina elongate, sinuous, extends slightly anterior to vestibule with short recurrent section; egg ellipsoidal.

Remarks

Cloacina theope sp. nov. differs from congeners in having three oesophageal denticles in the preneural region of the oesophagus which are at the same level, but are of dissimilar sizes. The dorsal denticle is well developed but the subventral denticles are mere thickenings of the oesophageal lining and may not warrant the designation as denticles. In all other species with three denticles at the same level in the oesophagus, *C. daveyi*, *C. eurynome*, *C. hera*, *C. hermes*, *C. hestia*, the denticles are equally developed, although in *C. hestia* and *C. eurynome* all three denticles may be weakly sclerotised. *C. theope* differs from *C. daveyi*, which has submedian cephalic papillae in which the distal segment is large and directed medially, and from all the remaining species, which have the deirid in the anterior oesophageal position and six rather

than eight leaf crown elements. It is most similar to *C. eurynome* from which it differs principally in having shorter spicules (3.57–3.98 (3.77) mm in *C. eurynome*, 2.29–2.63 (2.52) mm in *C. theope*).

If the subventral denticles are excluded from consideration, then the unornamented anterior oesophagus, a symmetrical buccal capsule with a smooth anterior margin, and the presence of a dorsal denticle indicates similarities with *C. cornuta*, *C. dindymene*, *C. dirce*, *C. ernabella*, *C. longispiculata* and *C. sciron*. *C. ernabella* differs in the shape of the cephalic papillae (globose, medially directed distal segment in *C. ernabella*), while all species except *C. sciron* differ in having the deirid in the anterior oesophageal region rather than at the level of the nerve ring. *C. theope* differs from *C. sciron*, which has an anteriorly arched buccal capsule, longer spicules (2.83–3.30 (3.00) mm in *C. sciron*, 2.29–2.63 (2.52) mm in *C. theope*), a longer dorsal ray and a vagina which is not recurrent. In *C. theope* the recurrent section of the vagina is twisted around the ascending arm in a manner similar to that found in *C. syphax* and *C. eurynome*. *C. theope* differs from *C. syphax* in the shape of the buccal capsule, which has an undulating anterior margin in *C. syphax* but is straight in *C. theope*. Therefore, *C. theope* is clearly distinguishable from all congeners.

DISCUSSION

The new records and new species reported in this paper suggest that a diverse array of species of *Cloacina* exists in macropodid marsupials in Papua New Guinea. Conclusions need to be guarded as the current collections have been obtained from a small number of individuals of each host species, in some instances from a single animal. As yet, there have been no comprehensive surveys of New Guinean macropodids for parasites, and several species of *Thylogale*, *Dorcopsis*, *Dorcopsulus* and *Dendrolagus* have apparently yet to be examined for helminths (Spratt *et al.* 1991). In addition, Beveridge (1998) and Beveridge and Speare (1999) have listed museum records of additional undescribed species from some of these hosts which cannot currently be named due to lack of adequate material.

In spite of the relatively rudimentary knowledge of the New Guinean parasite fauna, some preliminary comparisons can be made with species present in Australia. In terms of morphological characters, the species of *Cloacina* present in New

Guinea are virtually as diverse as those present in Australia. Of the various morphological features of the genus, only the spiral twisting of the proximal, recurrent region of the vagina (*C. syphax*, *C. eurynome*, *C. theope*) and the presence of amphids on conical projections (*C. praxithea*, *C. sappho*) appear to be restricted to species from New Guinea. Two other apparently autapomorphic characters, using *Arundelia dissimilis* (Johnston & Mawson, 1939) as an outgroup, are the posterior position of the amphids in *C. praxithea* and the dorsal deviation of the head in *C. polymela*. *A. dissimilis* is the sole member of a closely related genus within the tribe Cloacininae (see Beveridge 1987) and is therefore considered to be an appropriate outgroup for polarising morphological characters. Characters such as the origin of the external branchlets of the dorsal ray anterior to the major bifurcation are more common in species from New Guinea, but are also found in species from northern Australia. No obvious patterns are detectable in the distribution of other characters. While only tentative conclusions can be drawn in the absence of a formal phylogenetic analysis, there do not appear to be any major distinctions which can be drawn between species occurring in New Guinea compared with those present in Australia.

In several instances (*C. australis*, *C. cloelia*, *C. cornuta*, *C. cybele*, *C. dahli*), the same species of *Cloacina* are found in Australia and in New Guinea, a phenomenon explicable in terms of host distribution. *C. australis* and *C. cornuta* are both parasites of *M. agilis*, a wallaby which is common in northern Australia (Strahan 1995) and which invaded southern New Guinea relatively recently from Australia (Flannery 1995). Similarly, *C. cloelia*, *C. cybele* and *C. dahli* occur in pademelons of the genus *Thylogale*, and at least one species, *T. stigmatica*, is thought to be a recent arrival in New Guinea (Winter 1997). However, the occurrence of these same nematodes in species of *Thylogale* restricted to New Guinea suggests that they have been present for a longer period of time than the recent invasion of *T. stigmatica*.

The remaining species of *Cloacina* currently described from New Guinea occur in hosts which are endemic. Species of scrub wallabies *Dorcopsis* and *Dorcopsulus* do not occur in Australia, while the tree kangaroos, *Dendrolagus* spp., have apparently radiated in New Guinea and invaded north-eastern Australia secondarily (Flannery et al. 1996). The recent arrival of the genus *Dendrolagus* in Australia may have contributed to the absence of species of *Cloacina* in *D. lumholtzi* and *D. bennettianus*.

While the records of species of *Cloacina* from New Guinea are still fragmentary, it appears that a substantial New Guinean fauna exists, and its relationships with its hosts and the comparisons that can be made with Australian representatives may provide insights into the evolution and hence the diversity of this nematode genus.

KEY TO SPECIES OF *CLOACINA* IN MACROPODIDS FROM PAPUA NEW GUINEA

1. — Denticles present in preneural region of oesophageal lumen 2
— Denticles absent 13
2. — Paired ventral oesophageal denticles anterior to dorsal denticle *C. dahli*
— Single dorsal denticle, or three denticles at same level in oesophagus 3
3. — Anterior part of oesophagus lined with sclerotised bosses 4
— Anterior oesophagus without sclerotised bosses 8
4. — Anterior oesophageal bosses much larger than other bosses; deirid anterior to nerve ring; female tail swollen *C. australis*
— Oesophageal bosses of similar size; deirid at level of nerve ring or posterior to it; female tail not swollen 5
5. — Buccal capsule symmetrical in lateral view *C. erigone*
— Buccal capsule asymmetrical in lateral view, more shallow on dorsal aspect ... 6
6. — Buccal capsule prominently arched anteriorly *C. hyperea*
— Buccal capsule not prominently arched anteriorly 7
7. — Spicules 1.30–1.58 mm; distal segment of submedian papilla less than 1/4 length of proximal segment *C. procris*
— Spicules 1.67–2.07 mm; distal segment of submedian papilla only slightly shorter than proximal segment *C. sterope*
8. — Dorsal denticle and 2 vestigial subventral denticles present 9
— Single dorsal denticle present 10
9. — Spicules 3.57–3.98 mm *C. eurynome*
— Spicules 2.29–2.63 mm *C. theope*
10. — Prominent lips present *C. oweni*
— Lips absent 11
11. — Deirid at level of nerve ring; anterior margin

- of buccal capsule arched *C. sciron*
- Deirid in anterior oesophageal region, anterior margin of buccal capsule horizontal 12
12. — Cervical cuticle and female tail inflated, distal segment of submedian papilla almost as long as proximal segment, spicules 1.38–1.62 mm *C. cornuta*
- Cervical cuticle and female tail not inflated, distal segment of submedian cephalic papilla much shorter than proximal segment, spicules 1.84–2.26 mm *C. papuensis*
13. — Anterior margin of buccal capsule undulate 14
- Anterior margin of buccal capsule not undulate 18
14. — Amphids on or forming conical elevations projecting beyond cephalic collar 15
- Amphids embedded within cephalic collar 16
15. — Head deviated dorsally, cephalic collar elevated between adjacent submedian papillae *C. polymela*
- Head directed anteriorly, cephalic collar depressed between adjacent submedian papillae *C. sappho*
16. — External branchlets of dorsal ray arise before major bifurcation *C. syphax*
- External branchlets of dorsal ray arise after major bifurcation 17
17. — Cervical cuticle prominently inflated, submedian papillae project prominently beyond cephalic collar *C. solon*
- Cervical cuticle not inflated, submedian papillae very small, barely project above cephalic collar *C. solymus*
18. — External branchlets of dorsal ray arise before major bifurcation 19
- External branchlets of dorsal ray arise after major bifurcation 21
19. — Deirid anterior to nerve ring *C. cunctabunda*
- Deirid posterior to nerve ring 20
20. — Spicule length 2.34–2.97 mm *C. cretheis*
- Spicule length 1.23–1.45 mm *C. caballeroi*
21. — Buccal capsule sinuous in apical views, appearing as extra thickenings of wall in lateral or dorso-ventral views *C. sancus*
- Buccal capsule not sinuous in apical views 22
22. — Buccal capsule prominently arched anteriorly *C. nephele*
- Buccal capsule not prominently arched 23
23. — Amphids posterior to anterior margin of buccal capsule *C. praxithea*
- Amphids anterior to anterior margin of buccal capsule 24
24. — Oesophagus with sclerotised bosses, spicule tip foot-shaped *C. cloelia*
- Oesophagus lacking bosses, spicule tip simple 25
25. — Spicule length 3.90–5.05 mm, spicule tip simple *C. hecale*
- Spicule length 2.30–2.90 mm, spicule tip with enlarged flange, ala terminating abruptly anterior to spicule tip *C. cybele*

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DARWIN FORMATION (EARLY CRETACEOUS, NORTHERN TERRITORY) MARINE REPTILE REMAINS IN THE SOUTH AUSTRALIAN MUSEUM

BENJAMIN P. KEAR

Summary

Marine reptile remains from Early Cretaceous (Aptian/Albian) deposits of the Darwin Formation, Northern Territory, are described from the collections of the South Australian Museum. The material includes vertebra and limb girdle elements from ichthyosaurs and plesiosauroids, as well as the first described remains from the Northern Territory. The pliosaurid specimen (a single femur) is attributed to the small-bodied (up to 3 m in length) freshwater/near-shore marine taxon *Leptocleidus*, supporting interpretation of the Darwin Formation as representing a near-shore marine depositional environment. A comparison of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deposits elsewhere in Australia, indicates greatest compositional similarity to the Hauterivian-Barremian Birdrong Sandstone fauna of Western Australia. A potential link between the distribution of some marine reptile taxa (eg pliosaurids) and the prevailing depositional environment is also suggested.

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KEAR, B. P. 2002. Darwin Formation (Early Cretaceous, Northern Territory) marine reptile remains in the South Australian Museum. *Records of the South Australian Museum* 35(1): 33–47.

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Sometime in the 1960s (exact date unknown), a small collection of fossil marine reptile remains from the Early Cretaceous (Aptian/Albian) deposits of Casuarina Beach, Darwin Formation, Northern Territory (see Murray 1987, Fig. 1, p. 95 for locality map) was donated to the South Australian Museum. In 1994 several additional Darwin Formation marine reptile specimens were acquired as part of an exchange with the Museum and Art Gallery of the Northern Territory. A recent examination of these remains, which include isolated elements from both ichthyosaurs and plesiosauroids, has also revealed the presence of a pliosaurid femur. This specimen is attributable to the genus *Leptocleidus* Andrews, 1922 and represents the first documented pliosaur material from the Northern Territory. This paper describes Darwin Formation marine reptile remains currently housed in the South Australian Museum and provides a brief palaeoecological analysis based on faunal comparison with other known Early Cretaceous marine reptile bearing deposits.

Marine reptile remains were first reported from the Darwin Formation by an anonymous author (1924) who described a fragmentary ichthyosaur skeleton from Fannie Bay near Darwin. This specimen was later attributed to *Ichthyosaurus australis* (Tiechert & Matheson 1944); however,

Murray (1985) re-assigned the material, along with other ichthyosaur remains from Nightcliff, north of Fannie Bay, to *Ichthyosaurus* gen. et sp. indet. A more recent examination by Wade (1990) suggested that all ichthyosaur material from the Darwin Formation might be synonymous with *Platypterygius longmani* from the Aptian–Albian of Queensland. Murray (1987) described isolated ichthyosaur and elasmosaurid remains from Casuarina Beach, assigning the material to *Platypterygius* sp. and *Elasmosauridae* gen. et sp. indet., respectively. The presence of elasmosaurid and pliosaurid remains in the Casuarina Beach deposits was also noted by Cruickshank et al. (1999) but no descriptions were provided.

A comparison of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deltaic-marine deposits elsewhere in Australia (Wallumbilla Formation [Doncaster Member], Allaru Mudstone, Toolebuc Formation and Mackunda Formation, Queensland; Bulldog Shale, South Australia; Wallumbilla Formation [Doncaster Member], New South Wales; Birdrong Sandstone and Barrow Group, Western Australia) indicates greatest compositional similarity to the Hauterivian–Barremian Birdrong Sandstone fauna, with ichthyosaurs, elasmosaurids and the small-bodied pliosaurid *Leptocleidus* represented. A potential link between the distribution of some

marine reptile taxa (eg pliosaurids) and the prevailing depositional environment is also suggested. The presence of *Leptocleidus*, a pliosaurid genus known otherwise from freshwater and near-shore marine deposits (Andrews 1911, 1922; Strömer 1935; Cruickshank 1997; Cruickshank & Long 1997; Cruickshank et al. 1999) supports interpretation of the Darwin Formation as representing a shallow near-shore marine depositional environment (*sensu* Smart & Senior 1980; Murray 1985; Henderson 1998).

MATERIALS AND METHODS

Institutional abbreviations used: SAM, South Australian Museum, Adelaide; NTM, Museum and Art Gallery of the Northern Territory, Darwin; AM, Australian Museum, Sydney.

Lithostratigraphic nomenclature follows Mory (1988) for Early Cretaceous deposits of the Darwin area and Burton & Mason (1998) for the opal-bearing sediments of White Cliffs, New South Wales. Systematic terminology follows Montani (1999) for Ichthyopterygia and Brown (1981) for Plesiosauria except in the subdivision of Pliosauroida, in which Polycotylidae is retained as a separate family (*sensu* Williston 1925; White 1940; Persson 1963; Welles 1962; Carpenter 1996, 1997). Functional sub-division of the vertebral column in ichthyopterygians follows Buchholtz (2001), with designation of structural units as neck, trunk, tail stock and fluke. Interpretation of plesiosaur pelvic and femoral musculature follows Robinson (1975) and Lingham-Soliar (2000). All measurements were taken using callipers and are in millimetres (mm).

GEOLOGICAL SETTING AND PRESERVATION

The marine reptile-bearing deposits of the Darwin Formation are typically characterised by glauconitic sandstone and radiolarian mudstone with basal quartzose conglomerate and localised nodular phosphorite horizons (Henderson 1998). The unit forms part of the Bathurst Island Group, which rests nonconformably on Precambrian basement within the Money Shoals Platform (see Fig. 1, p. 117 and Fig. 6, p. 124 of Henderson 1998 for locality and stratigraphic setting). At its base, the Bathurst Island Group is composed of the laterally equivalent Darwin Formation and Marligar Formation, which are overlain in turn by the Wangarlu Mudstone and Moonkinu

Formation.

The Darwin Formation has historically been considered Albian in age on the basis of its macroinvertebrate (Day 1969; Skwarko 1966, 1968; Henderson 1990) and palynomorph (Morgan 1980) assemblages; however, more recent analyses (Henderson 1998; D. Megirian pers. comm. 2000) suggest an upper Aptian age. The Marligar Formation has been dated as Neocomian/Aptian by palynological studies (Burger 1978) and upper Aptian because of its laterally equivalent relationship with the Darwin Formation (Henderson 1998). The overlying Wangarlu Mudstone is regarded as upper Albian–Cenomanian (possibly with a basal lower Albian component, Henderson 1998) on the basis of ammonite (Henderson 1990) and palynological (Norvick & Burger 1975; Burger 1978) data. The uppermost Moonkinu Formation is considered Cenomanian–Turonian on account of its ammonite (Wright 1963) and bivalve/gastropod/scaphopod (Skwarko 1983) faunas.

The glauconitic sandstones and predominant radiolarian mudstones of the Darwin Formation reflect a near-shore marine/paralic depositional environment (Smart & Senior 1980; Henderson 1998). The presence of a limited benthic invertebrate fauna also suggests unfavourable, possibly anoxic bottom conditions (Henderson 1998).

The Darwin Formation marine reptile remains generally occur as heavily weathered isolated elements, although several fragmentary skeletons have been recovered (Murray 1985; D. Megirian pers. comm. 2000). The disarticulated nature of the remains led Murray (1985) to speculate that an inshore and/or tidal depositional environment may have facilitated stranding of decaying carcasses on mudflats prior to burial.

SYSTEMATICS

DIAPSIDA Osborn, 1903

ICHTHYOPTERYGIA Owen, 1860

ICHTHYOSAURIA de Blainville, 1835

OPHTHALMOSAURIA Appleby, 1956 (*sensu* Montani 1999)

Platypterygius von Huene, 1922

cf. Platypterygius longmani

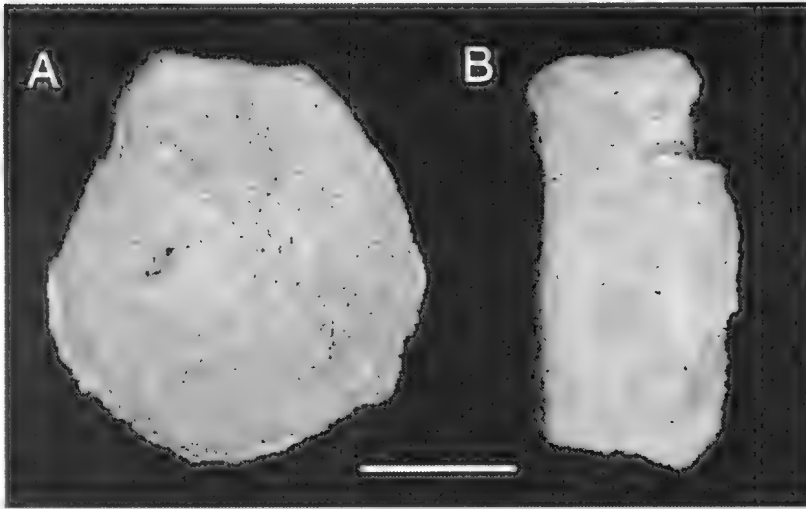


FIGURE 1. SAM P35039, *cf. Platpterygius longmani* dorsal vertebra in (A) anterior and (B) lateral views. Scale bar is 40 mm.

Material

SAM P35039 (Figs 1A, B; Table 1), four associated mid-posterior trunk vertebral centra; SAM P35426 (Table 1), two articulated anterior

trunk centra; SAM P35427 (Table 1), three associated anterior tail stock centra; SAM P35429 (Table 1), two associated sections of eight and four articulated anterior? tail stock centra; SAM

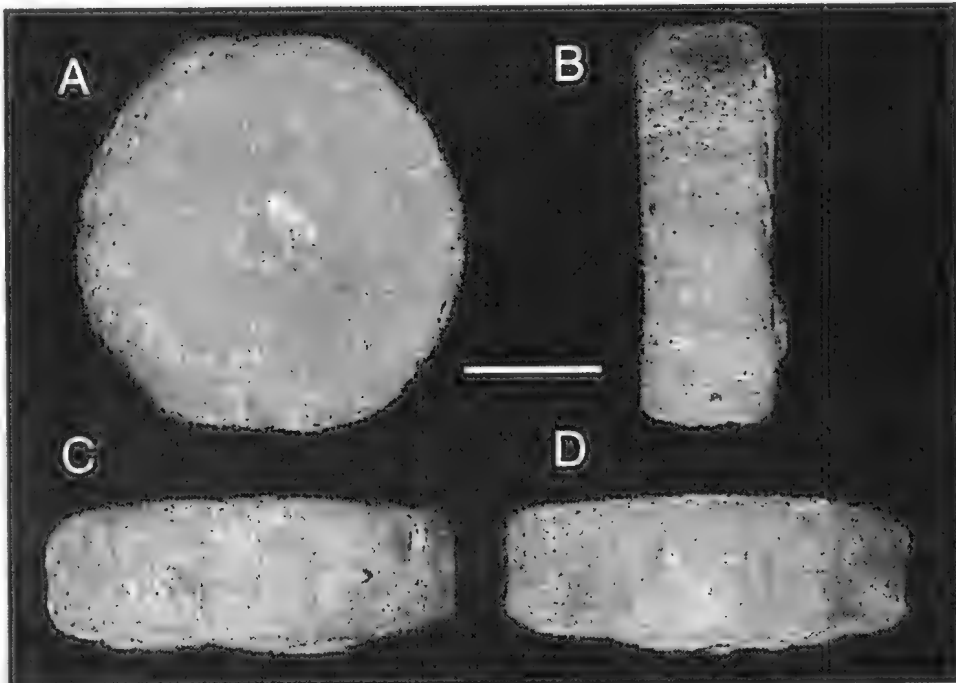


FIGURE 2. SAM P35430, *cf. Platpterygius longmani* caudal vertebra in (A) anterior, (B) lateral, (C) ventral and (D) dorsal views. Scale bar is 20 mm.

TABLE 1. Measurements (mm) of *cf. Platypterygius longmani* vertebral centra from the Darwin Formation, Northern Territory.

Specimen	Length	Width	Height
SAM P35039	39.6	91.2	98.9
	33.1	88.9	90.2
	30.2	80.1	89.2
	32.3	62.6	66.1
SAM P35426	40.6	85.5	88.9
	37.0	86.1	89.7
SAM P35427	40.7	94.0	96.4
	30.1	86.2	92.4
	25.8	102.8	109.6
*SAM P35429	24.9	81.6	69.9
	25.8	83.1	75.2
	26.4	86.4	79.1
	25.2	64.8	83.9
	20.5	—	78.2
	21.6	58.3	60.1
	21.1	58.9	50.8
	22.3	—	57.2
	17.4	—	55.1
	18.9	—	46.6
	14.1	—	46.9
	—	—	—
SAM P35430	20.8	68.9	59.7
	20.8	61.1	62.1
	18.7	55.7	56.1
	14.6	53.2	50.4
	15.3	47.9	48.3
	15.3	42.8	42.6
	15.2	43.6	45.0
	12.9	41.5	41.3

* some centra represented by fragments only

P35430 (Figs 2A, B, C, D; Table 1), nine associated anterior tail stock centra (juvenile).

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

All of the preserved centra are disc-like and anteroposteriorly compressed, with the dorsal length subequal to the ventral. Tail stock centra (Figs 2A, B, C, D) exhibit a more marked degree of anteroposterior compression relative to those from the trunk region (Figs 1A, B) and are slightly

ovoid in outline, with height being approximately 1.5 times the transverse width. The articular surfaces of all centra are deeply amphicoelous, with a distinct central notochordal pit. The neural canal is generally broad and shallow, becoming narrower in centra from the tail stock region. The neural arch facets are narrow and rectangular in all centra. Where preserved, both the diapophyses and parapophyses of the trunk centra are distinctly raised and subcircular. This is unlike centra from the tail stock region, in which only the ovoid diapophysis is present and positioned low on the lateral centrum surface. The ventral surfaces of at least two of the recovered centra from the tail stock region show distinct haemal arch facets. These are slightly concave and saddle-shaped in outline with low ridge-like margins. Medially, the haemal arch facets border the very weakly concave, spool-shaped depression for the haemal canal.

Remarks

All of the ichthyosaur vertebral centra examined can be distinguished from those of basal ichthyopterygians by their disc-like shape and strong anteroposterior compression (the more plesiomorphic Grippidia having cylindrical centra, Montani 1999). The absence of any further diagnostic features restricts attribution of the specimens to Ichthyosauria gen. et sp. indet. However, tentative assignment of the remains to *cf. Platypterygius longmani* is justifiable on the basis of: 1) overall similarity to *P. longmani* vertebral material described from the Allaru Mudstone and Toolebuc Formation, Queensland (Wade 1990) and Darwin Formation (Murray 1985, 1987 *sensu* Wade 1990); and 2) current recognition of *P. longmani* as the only valid ichthyosaur species from the Aptian–Albian of Australia (Wade 1990; Bardet et al. 1994; Arkhangelsky 1998; Montani 1999).

Buchholtz (2001) discussed differentiation of structural units within the vertebral column of Jurassic ichthyosaurs with relation to variation in swimming styles between taxa. Following on from this study, it can be suggested that differences observed in the Darwin Formation centra (relating to regionalised morphological variation along the vertebral column) can be used to predict preferred swimming style in the Cretaceous *P. longmani*. The marked increase in height proportionate to width, and anteroposterior compression of the tail stock relative to trunk centra, in the Darwin Formation specimens is comparable to the condition recorded in derived thunniform-model

ichthyosaurs such as *Ophthalmosaurus icenicus* and *Stenopterygius quadrissicus* (Buchholtz 2001). Wade (1990) and Broili (1907) noted that the anterior fluke centra in *P. longmani* and *P. platydactylus* were distinctly higher than wide, a feature also conforming to the predicted thunniform condition. Taken together therefore, these characteristics may suggest that *Platypterygius* spp. employed an axial oscillatory swimming mode and probably shared many other key traits (see Montani 1999; Buchholtz 2001) with derived thunniform-model ichthyosaurs.

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

Plesiosauroida gen. et sp. indet.

Material

SAM P35431 (Figs 3A, B, C), incomplete and badly weathered element tentatively identified as the ventral plate portion of a left ischium. Orientation is based on position of the lateral margin and its attitude relative to the horizontal axis; SAM P35434 (Figs 4A, B, C), right ischium lacking part of anteromedial margin.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

Dimensions of remains are: SAM P35431, total length of 96.7 mm; total width is 98.9 mm; maximum height is lateral extremity is 22.5 mm; maximum length of lateral extremity is 55.3 mm; maximum height of ventral plate is 45.9 mm. SAM P35434, total length is 74.6 mm; total width

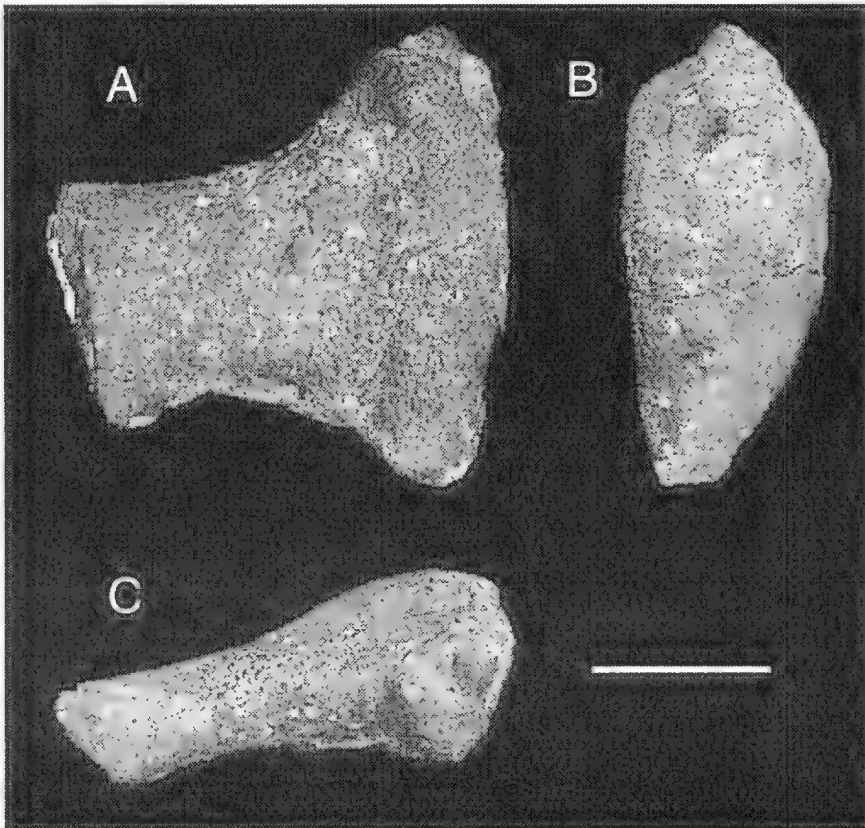


FIGURE 3. SAM P35431, *Plesiosauroida* gen. et sp. indet. partial ischium in (A) dorsal, (B) medial and (C) posterior views. Scale bar is 40 mm.

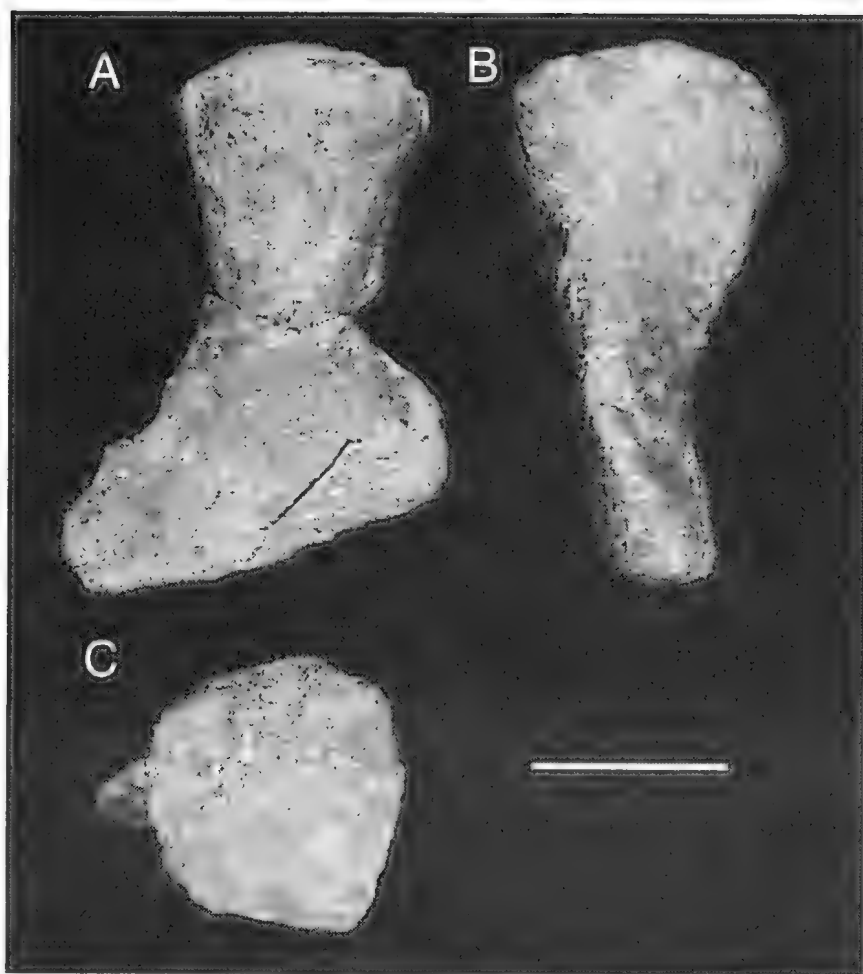


FIGURE 4. SAM P35434, *Plesiosauroidea* gen. et sp. indet. ischium in (A) dorsal, (B) posterior and (C) lateral views. Scale bar is 40 mm.

is 97.4 mm; maximum height of the of lateral articular surface is 52.1 mm; maximum length of lateral articular surface is 46.1 mm; maximum height of ventral plate is 10.8 mm. Both SAM P35431 and SAM P35434 are hatchet-shaped in dorsal outline with an anteroposteriorly expanded ventral plate. The lateral articular extremity of SAM P35434 is massive but has been lost in SAM P35431. Medially, the ventral plate portion of both elements is dorsoventrally compressed with an inclined medial edge for contact with the opposing ischium. This surface is oriented approximately 10° ventral to a horizontal plane through the lateral articular extremity, and is deeply pitted, suggesting the presence of cartilage. Both the dorsal and ventral surfaces of the ventral

plate in SAM P35434 are rugose, possibly for attachment of the m. puboischiofemoralis internus and m. p. externus, respectively. A weak ridge on the posteromedial margin of the ventral plate may also have supported slips of the m. ischioatrochantericus. The ventral plate of both specimens is not greatly anteroposteriorly expanded (with total length being just slightly less than the total transverse width of each element) and is separated from the lateral articular extremity by a constricted waist-like midsection. This is ovoid to circular in cross-section, becoming increasingly dorsoventrally thickened towards the lateral articular surface (not preserved in SAM P35431). The articular surface itself is convex, with the rectangular anterior pubis facet

offset approximately 195° relative to the longitudinal axis of the articular surface. The pubis facet is separated posteriorly from the rectangular median acetabular facet, and in turn from the lobate posterior-most ilial facet (offset approximately 150° relative to the longitudinal axis of the articular surface) by weak parallel ridges. The articular surface margin is produced into a crenate rim, which is continuous ventrally, with a low rugose tuberosity possibly marking part of the m. puboischiofemoralis internus attachment.

Remarks

Despite being heavily weathered, SAM P35431 is identified as the ventral plate portion of a plesiosaurian left ischium on the basis of its hatchet-shaped outline and general morphology. Nevertheless, the specimen is unusual in its markedly dorsoventrally deep, medial articular margin. SAM P35431 was initially registered as an ichthyosaurian humerus belonging to *Platypterygius* sp. However, such an identification is unlikely as the humeri of *Platypterygius* spp. are much more robust, with rectangular to spool-shaped dorsal outline and prominent ridge-like tuberosities on both the dorsal and ventral surfaces (eg Kiprijanoff 1881; Broili 1907; Kuhn 1946; McGowan 1972; Wade 1984; Murray 1987; Choo 1999). SAM P35431 also differs from the larger girdle elements of *Platypterygius* spp., in which the coracoid is subcircular in outline with dorsoventrally deep glenoid/intercoracoid facets (Broili 1907; Wade 1984), and both the scapula and ischiopubis are strap-like with predominantly narrow, ridge-like articular surfaces (Broili 1907; Nace 1939; Murray 1987).

SAM P35434 probably represents a juvenile individual because of its small size and poor ossification of the articular surfaces. Both it and SAM P35431 can be assigned to Plesiosauroidea on the basis of their anteroposteriorly short ventral plates. This differs from the condition in pliosauroids in which the ventral plate of the ischium bears a marked posterior expansion (Mehl 1912; Andrews 1913; Tarlo 1959, 1960; Brown 1981). The presence of a relatively weak posterior expansion in *Eurycleidus* (Cruickshank 1994) and *Leptocleidus* (pers. obs, AM F99374 from the Aptian-Albian Bulldog Shale of Coober Pedy, South Australia), however, suggests that this character state may not be universal for the group. SAM P35434 is unusual in its proportionately massive articular head relative to the ventral plate.

The phylogenetic significance of this feature, if any, is uncertain because of its immature stage of development.

ELASMOSAURIDAE Cope, 1869

Elasmosauridae gen. et sp. indet.

Material

SAM P35432 (Figs 5A, B, C, D), a single weathered posterior cervical vertebral centrum.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

The surface of the centrum is badly weathered with very little periosteal bone remaining. Total length is 72.8 mm; width of anterior surface is 109.5 mm; depth of anterior surface is 85.2 mm. In general proportions, the centrum is anteroposteriorly short relative to both the height and width of the anterior articular surface. Both the lateral and ventral surfaces are shallowly concave, with the ventral surface being pierced by two large foramina. The articular surfaces are poorly preserved but clearly platycoelous, with a raised convex rim. The neural arch facets are indistinct but prominent bosses high on the lateral surface of the centrum indicate positioning of the rib facets.

Remarks

SAM P35432 is tentatively assigned to *Elasmosauridae* on the basis of its platycoelous articular surfaces. Murray (1987) reported an elasmosaurid cervical with very shallowly concave articular facets from the Casuarina Beach locality. Brown (1981, 1993) and Bardet et al. (1999) regarded the presence of platycoelous articular surfaces on the cervical centra to be a potential synapomorphy for *Elasmosauridae*. The character state has also been recorded in the Maastrichtian cryptoclidid *Morturneria* (Chatterjee & Small 1989), though Bardet et al. (1991) suggested that this taxon may represent a derived elasmosaurid.

The proportionately short centrum length relative to height of SAM P35432 differs from the common condition in elasmosaurids (such as that described by Murray 1987), in which the cervical centra are markedly elongate (Brown 1993; Bardet et al. 1999). The presence of relatively short cervical centra is considered plesiomorphic among

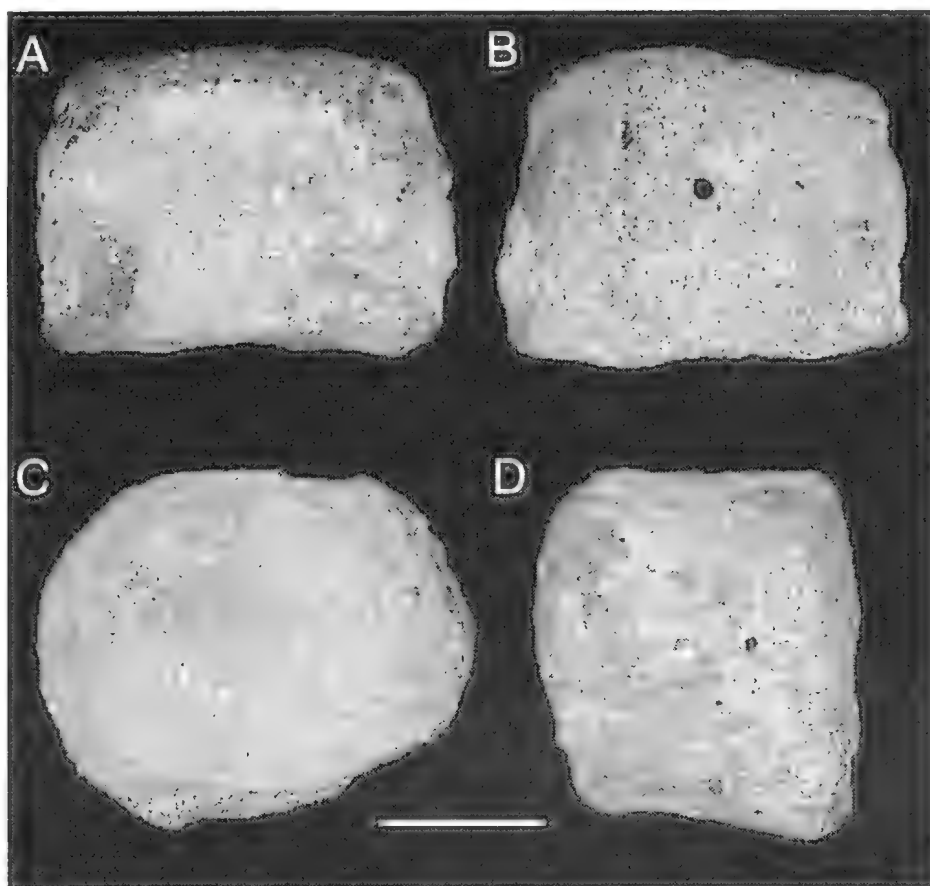


FIGURE 5. SAM P35432, Elasmosauridae gen. et sp. indet. posterior cervical centrum in (A) dorsal, (B) ventral, (C) anterior and (D) lateral views. Scale bar is 40 mm.

plesiosauroids (Brown 1993; Bardet *et al.* 1999). However, the feature has been described in the potential elasmosaurid taxa (*sensu* Bardet *et al.* 1991) *Aristonectes* (Cabrera 1941) and *Morturneria* (Chatterjee & Small 1989) as well as in indeterminate elasmosaurid posterior cervicals from unspecified (probably Albian) deposits near Oodnadatta (Freytag 1964) and the Neales River region (SAM P6181, Persson 1960), South Australia; Toolebuc Formation, Queensland (Kear 2001); and Molecap Greensand, Western Australia (Long & Cruickshank 1998). The presence of proportionately elongate cervicals may therefore not necessarily be universal amongst elasmosaurids, with some taxa exhibiting relatively short centra, particularly in the posterior cervical region.

SAM P35432 is notable for its possession of a raised convex rim surrounding the central

concavity of the articular surface. Brown *et al.* (1986) and Brown (1993) considered this a plesiomorphic condition commonly associated with members of the Cryptoclididae and Plesiosauridae. In contrast, elasmosaurids, including basal taxa such as *Occitanosaurus* (Bardet *et al.* 1999) and *Muraenosaurus* (Andrews 1910; Brown 1981, 1993), generally exhibit a more open V-shape, in which the articular surface margins form an abrupt angle with the centrum sides. A similar trait is evident in elasmosaurid material from the Toolebuc Formation of Queensland (Kear 2001), and is indicated (but not described) in the figured Darwin Formation specimen (NTM P8727-70, Fig. 1, p. 97) of Murray (1987). Carpenter (1996), however, considered articular rim morphology to be a variable character amongst plesiosaurs and of questionable diagnostic value.

PLIOSAUROIDEA Seeley, 1874

PLIOSAURIDAE Seeley, 1874

Leptocleidus Andrews, 1922

Leptocleidus sp.

Material

SAM P35053, cast of NTM P913-5 (Figs 6A, B, C) right femur.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

A near complete right femur lacking part of posterodistal margin. Total length is 260.8 mm;

total proximal length is 47.9 mm; total proximal height (including trochanter) is 51.5 mm; width across base of dorsal trochanter is 37.2 mm; total distal length (not including missing posterior margin) is 91.6 mm; total distal height is 25.9 mm. The anterior edge of the femur is weakly sigmoidal, with a strongly convex distal extremity. The posterior edge is uniformly concave along its entire length. Both the dorsal and ventral surfaces are shallowly concave along their longitudinal axis; however, the ventral surface becomes convex and upturned towards the distal extremity. Proximally, the femur is greatly dorsoventrally expanded and separated from its distal section by a constricted neck. The dorsal trochanter is robust and anteroposteriorly constricted at its base. It is separated from the ovoid glenoid articular surface by a shallow groove. The surfaces of both the dorsal trochanter and glenoid articulation are deeply pitted, suggesting the presence of cartilage.

The femoral shaft is weakly anteroposteriorly constricted and ovoid in cross-section, with its posterior margin bearing a raised rugose tuberosity, possibly for attachment of the *m. caudifemoralis*. A second low tuberosity is present on the median ventral surface and may represent part of the *m. puboischiofemoralis* insertion. The distal femoral extremity is fan-shaped in dorsoventral outline, with a weakly projecting anterodistal margin. The distal articular surface is narrow and elliptical, with a raised median ridge separating the very large radial facet from the remains of the ulnar facet.

Remarks

Despite the poor existing knowledge of femoral morphology in *Leptocleidus* spp., SAM P35053 (NTM P913-5) can be readily distinguished from the proportionately shorter and stouter propodials of elasmosaurids (Brown 1981; Murray 1987) by its anteroposteriorly broad, flat femoral shaft, greatly expanded distal extremity and sigmoidal anterior margin. These characteristics are very similar to those of the fragmentary femora of *L. capensis* (Andrews 1911) and well-preserved material (AM F99374, SAM P15980) from the Bulldog Shale of South Australia (Figs 7A, B). The femur of *L. clemai* (Cruickshank & Long 1997) differs in its possession of a concave anterior margin. This feature, along with a proportionately more slender shaft, is also present in the femora of polycotylids and most other pliosauroids (Andrews 1913; Welles 1943, 1962; Brown 1981; Storrs 1999). A sigmoidal anterior femoral and humeral margin has, however, been



FIGURE 6. SAM P35053 (cast of NTM P913-5), *Leptocleidus* sp. femur in (A) anterior, (B) dorsal and (C) proximal views. Scale bar is 40 mm.

TABLE 2. Marine reptile groups from Early Cretaceous deltaic-marine deposits of Australia. Pliosauroids are separated into small-bodied (eg *Leptocleidus*) and large-bodied (eg *Kronosaurus*) forms because of their differing ecological roles. The poorly known taxon '*Cimoliasaurus maccoyi*' is recorded separately because of its unknown affinity. Indeterminate plesiosaur material from the marine Bungil Formation, Queensland and freshwater deposits of the Griman Creek Formation, New South Wales, and Strzeleki and Otway Groups, Victoria is excluded pending a more thorough examination of the remains. Taxa from the opal bearing deposits of White Cliffs, New South Wales are placed within the Wallumbilla Formation in accordance with the lithostratigraphic nomenclature of Burton & Mason (1998). Source texts include: Etheridge (1904)¹, Longman (1924)², Tierchert & Matheson (1944)³, Persson (1960⁴, 1963⁵, 1982⁶), Ludbrook (1966)⁷, Condon (1968)⁸, Pledge (1980)⁹, Smart & Senior (1980)¹⁰, Gaffney (1981)¹¹, Molnar (1982¹², 1991¹³), Wade (1984¹⁴, 1990¹⁵), Murray (1985¹⁶, 1987¹⁷), Hocking et al. (1987)¹⁸, Burger (1988)¹⁹, Bardet (1992)²⁰, Thulborn & Turner (1993)²¹, Krieg & Rodgers (1995)²², Cruickshank & Long (1997)²³, Henderson (1998)²⁴, Long (1998)²⁵, Long & Cruickshank (1998)²⁶, Cruickshank et al. (1999)²⁷, Choo (1999)²⁸, Kear (2001)²⁹.

Darwin Formation (Money Shoals Platform) Aptian/Albian	Wallumbilla Formation (Eromanga Basin) Aptian-Albian	Allaru Mudstone (Eromanga Basin) Albian	Toolebuc Formation (Eromanga Basin) Albian
Ichthyosauria ^{3,13,15,16,17}	Ichthyosauria ¹³	Ichthyosauria ^{12,13,14,15,25}	Ichthyosauria ^{12,13,14,15,25}
Elasmosauridae ^{13,17}	Elasmosauridae ^{4,5,12,13,25}	Elasmosauridae ^{4,5,12,13,25}	Elasmosauridae ^{4,5,6,12,13,21,25,29}
Small pliosaurid ²⁷	Large pliosaurid ^{1,2,4,5,12,13,21,25} Polycotylidae ^{4,5,13} ' <i>C. maccoyi</i> ' ^{1,4,13}	Chelonioidae ^{13,25}	Large pliosaurid ^{2,4,5,12,13} Polycotylidae ^{21,25,27} Chelonioidae ^{11,12,13,25}
Shallow near-shore marine ²⁴ / paralic ¹⁰ / possibly tidal ¹⁶	Coastal / offshore shallow marine ^{10,19}	Shallow marine ¹⁰	Shallow marine ¹⁰

cited as a potentially diagnostic character state for the polycotylid genus *Polycotylus* (Storrs 1999).

DISCUSSION

The Darwin Formation sediments have been interpreted as representing a shallow near-shore marine/paralic (Smart & Senior 1980; Henderson 1998) to possibly tidal (Murray 1985) depositional environment. The presence of the small pliosaurid taxon *Leptocleidus*, known elsewhere from freshwater and near-shore marine deposits (Andrews 1911, 1922; Strömer 1935; Cruickshank 1997; Cruickshank & Long 1997; Cruickshank et al. 1999), is consistent with this interpretation.

A comparison (Table 2) of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deltaic-marine deposits elsewhere in Australia (Wallumbilla Formation [Doncaster Member], Allaru Mudstone, Toolebuc Formation and Mackunda Formation, Queensland; Bulldog Shale, South Australia; Wallumbilla Formation [Doncaster Member], New South Wales; Birdrong Sandstone and Barrow Group,

Western Australia) indicates greatest compositional similarity to the Hauterivian-Barremian Birdrong Sandstone fauna, with ichthyosaurs, elasmosaurids and the small-bodied pliosaurid *Leptocleidus* represented. Throughout the Early Cretaceous marine deposits, ichthyosaurs show a wide distribution (occurring in all currently recognised deposits except the Albian Mackunda Formation and unspecified Berriasian subsurface sediments of the Barrow Group), as do elasmosaurids, which have been recorded from all localities except those of the Albian Mackunda Formation and Berriasian Barrow Group.

Cruickshank et al. (1999) indicated the possible presence of cryptoclidids in the Aptian-Albian Bulldog Shale. This is supported by more recent observations of the South Australian fauna (Kear unpubl.) but as yet the group has not been recorded from any other Australian deposit.

The distribution of small- and large-bodied pliosaurid taxa in the Australian Early Cretaceous is variable, with smaller forms (represented by at least two species of *Leptocleidus*, Cruickshank et al. 1999) confined to the Darwin Formation,

TABLE 2. (cont.)

Mackunda Formation (Eromanga Basin) Albian	Bulldog Shale (Eromanga Basin) Aptian–Albian	Birdrong Sandstone (Carnarvon Basin) Hauterivian–Barremian	Barrow Group (Carnarvon Basin) Berriasian
Polycotylidae ¹³	Ichthyosauria ^{9,13,20} Elasmosauridae ^{9,27} Small pliosaurid ^{9,25,27} Large pliosaurid ⁹ Cryptoclididae? ²⁷	Ichthyosauria ^{3,13,28} Elasmosauridae ^{26,27} Small pliosaurid ^{23,27}	Small pliosaurid ²⁶
Paralic ¹⁰	Shallow marine ²² / offshore ⁷	Coastal near-shore shallow marine ¹⁸ / paralic ⁸	Fluviatile-deltaic ¹⁸

Bulldog Shale and Birdrong Sandstone. Larger pliosaurid remains occur only in the Aptian–Albian Wallumbilla Formation (Doncaster Member), Albian Toolebuc Formation and Bulldog Shale deposits. This division may be linked to the different habitat preferences and ecological roles of small- and large-bodied pliosaurid taxa, with offshore environments preferentially supporting larger-bodied forms. An exception is seen in the shallow offshore marine (Ludbrook 1966; Krieg & Rogers 1995) Bulldog Shale, which includes both small- and large-bodied pliosaurid remains (the latter being represented by an isolated tooth, SAM P22525, from the opal-bearing sediments of Coober Pedy, figured by Pledge 1980, p. 8).

Distribution of polycotylids in the shallow marine (Smart & Senior 1980; Burger 1988) Wallumbilla Formation, Toolebuc Formation and paralic (Smart & Senior 1980) Mackunda Formation may, as with large-bodied pliosaurids, be related to a preference for predominantly offshore marine environments. However, individuals also appear to have readily

frequented more inshore habitats, as suggested by their occurrence in the Mackunda Formation deposits.

Restriction of chelonoids to the upper Albian Allaru Mudstone and Toolebuc Formation may be the product of both the group's temporal distribution (the earliest-known chelonoid being recorded from the upper Aptian – lower Albian Santana Formation of Brazil, Hirayama 1997, 1998) as well as environmental factors such as prevailing water temperatures. Studies of sedimentary sequences (Frakes & Francis 1988; Frakes & Krassay 1992; Frakes et al. 1995; Constantine et al. 1998), climatic modelling (Barron & Washington 1982) and isotope data (Gregory et al. 1989; Pirrie et al. 1995) have suggested that strongly seasonal climates with winter freezing and at least seasonal sea ice characterised high latitudes in the Early Cretaceous of Australia. Such conditions may well have been unfavourable to chelonoids and provided an effective barrier to the group's dispersal into the Australian region prior to the upper Albian.

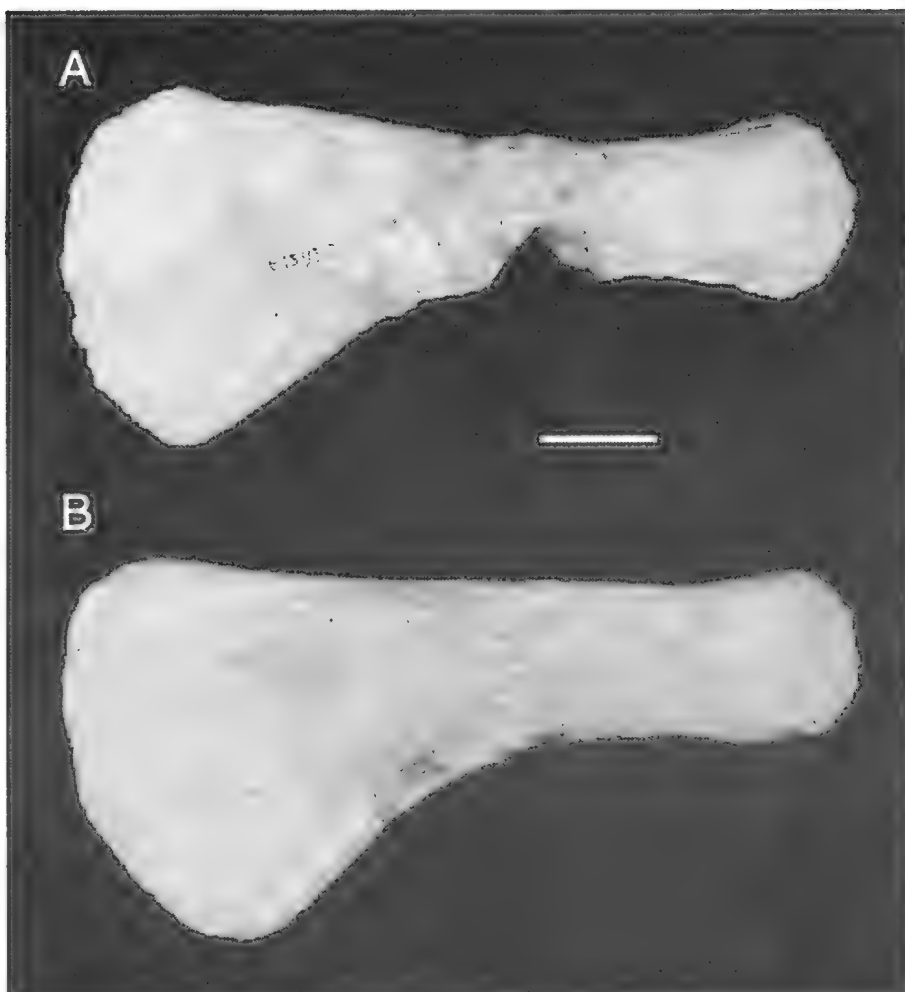


FIGURE 7. SAM P15980 juvenile *Leptocleidus* sp. humerus (A) and femur (B) from Andamooka, South Australia. Scale bar is 20 mm.

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TENTACULARIID CESTODES OF THE ORDER TRYPANORHYNCHA (PLATYHELMINTHES) FROM THE AUSTRALIAN REGION

H. W. PALM & I. BEVERIDGE

Summary

The present study summarises information on tentaculariid trypanorhynchs from Australian waters. A total of 19 species from the genera *Nybelina* Poche, 1926, *Heteronybelinia* Palm, 1999, *Mixonybelinia* Palm, 1999, *Kotorella* Euzet & Radujkovic, 1989 and *Kotorelliella* gen. nov. were identified: *N. aequidentata* (Shiple & Hornell, 1906); *Nybelina africana* Dollfus, 1960; *N. hemipristis* sp. nov.; *N. jayapaulazariahi* Reimer, 1980; *N. mehlhorni* sp. nov.; *N. schmidtii* Palm, 1999; *N. scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996); *N. strongyla* Dollfus, 1960; *N. thyrsites* Korotaeva, 1971; *N. victoriae* sp. nov.; *Heteronybelinia australis* sp. nov.; *H. estigmena* (Dollfus, 1960); *H. pseudorobusta* sp. nov.; *Mixonybelinia beveridgei* (palm, Walter, Schwerdtfeger & Reimer, 1997); *M. cribbi* sp. nov.; *M. edwinlintoni* (Dollfus, 1960); *M. southwelli* Palm & Walter, 1999; *Kotorella pronosoma* (Stossich, 1901) and *Kotorelliella jonesi* gen. et sp. nov. The new genus *Kotorelliella* is characterised by a homeocanthous, heteromorphous metabasal armature and a basal armature with additional interpolated hooks on the external surface of the tentacle, thus appearing heterocanthous. The new species appears to be closely related to *Kotorella pronosoma*. The tentaculariid trypanorhynch fauna in Australian waters is species rich, with 22 (48%) of the total of 46 known species occurring in waters of the region. Eleven new locality, and 20 new host records are reported.

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Palm (1999), Palm et al. (1997), Palm and Overstreet (2000) and Palm and Walter (1999, 2000) partially revised the trypanorhynch cestode family Tentaculariidae Poche, 1926 on the basis of material deposited in museums in London, Paris, Vienna and the United States. Following the erection of two new genera, *Heteronybelinia* Palm, 1999 and *Mixonybelinia* Palm, 1999 by Palm (1999), Palm and Walter (2000) gave a summary of the current state of knowledge within the tentaculariid trypanorhynch genera. Thus, to date, a total of 39 species of *Kotorella*, *Nybelinia*, *Heteronybelinia* and *Mixonybelinia* are considered valid (Palm & Walter 2000).

There is little known about the tentaculariid trypanorhynchs from Australian coastal waters. The first collections were made by a French scientific expedition under the command of Nicolas Baudin between 1801 and 1803 (Beveridge & Campbell 1996), but the cestodes, *Tentacularia coryphaenae* Bosc, 1797 and an

unidentified species of *Nybelinia* were not described until 1942 (Dollfus 1942). Korotaeva (1971) named the *Nybelinia* species of Dollfus (1942) *N. thyrssites* and subsequently (Korotaeva 1974) reported additional unidentified *Nybelinia* spp. from other fishes from southern Australia. Lester et al. (1988) and Sewell and Lester (1988) reported *Tentacularia* sp. from orange roughy, *Hoplostethus atlanticus* Collett, 1889 off the coasts of South Australia and Tasmania; while Sewell and Lester (1995) found *Nybelinia* sp. in jewfish, *Rexia solandri* (Cuvier & Valenciennes, 1832) from southern Australian waters. Beveridge and Campbell (1996) recorded *Tentacularia coryphaenae* Bosc, 1797, *Nybelinia thyrssites* Korotaeva, 1971 and *N. sphyrnae* Yamaguti, 1952 from Australian fishes; while Jones and Beveridge (1998) added *N. queenslandensis* from a carcharhinid shark as a new species. Palm (1999) recorded *Nybelinia lingualis* (Cuvier, 1817) from southern Australian waters and Speare (1999)

reported *Nybelinia* sp. from sailfish, *Istiophorus platypterus* (Shaw & Nodder, 1792) off the coast of Queensland. Thus, a total of five tentaculariid species has been described from Australia.

Last and Stevens (1994) summarised knowledge of the Australian chondrichthyan fauna, the definitive hosts of trypanorhynch cestodes, as being extremely rich and consisting of 296 species, 54% of them endemic. In terms of host-specificity and zoogeography of trypanorhynch cestodes, the Australian fauna might therefore harbour a high number of endemic and locally distributed tentaculariid trypanorhynchs, such as was observed within the related family Eutetrarhynchidae by Beveridge (1990). Palm (1999) and Palm and Walter (2000) suggested that many tentaculariids, for example *Tentacularia coryphaenae* and *Nybelinia lingualis*, exhibit a cosmopolitan or circumtropical distribution pattern. However, records from the south-west Pacific and south-east Indian Ocean are scarce. For example, the tentaculariids *Tentacularia coryphaenae*, *Nybelinia africana* and *N. scoliodoni* were only recently recorded from Indonesian coastal waters (Palm 2000). Other records which might confirm a wide distribution and possibly a low degree of host specificity for these trypanorhynchs are still lacking.

The present study was carried out to examine the species of *Nybelinia*, *Heteronybelinia*, *Mixonybelinia* and *Kotorella* deposited in museum collections in Australia as well as in the collection of the junior author. Where necessary, the specimens are described and illustrated as emendations to currently available descriptions. Apart from the establishment of new host and locality records, species identifications provide further insight into the zoogeographical distribution of tentaculariid cestodes. The comparison of the specimens with earlier descriptions allows comments to be made on the extent of intraspecific morphological variability within tentaculariid trypanorhynchs. Together with the study of deposited tentaculariids from other collections (Palm 1999; Palm & Overstreet 2000; Palm and Walter 1999, 2000), the present study summarises the current state of knowledge on the genera of tentaculariid cestodes.

South Australian Museum (SAM), Adelaide, as well as the Queensland Museum (QM), Brisbane. Special attention was given to unidentified specimens deposited simply as *Nybelinia* sp. Unmounted specimens were stained in Celestine Blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. Pieces of strobilae were embedded in paraffin, serial sections were cut at a thickness of 5 µm and stained with haematoxylin and eosin. Drawings were made using an Olympus BH2 microscope with an ocular micrometer and drawing tube. Terminology for morphological features peculiar to the Trypanorhyncha follows Dollfus (1942) and Campbell and Beveridge (1994).

The following measurements were made: scolex length (SL), scolex width at level of pars bothridialis (SW), pars bothridialis (pbo), pars vaginalis (pv), pars bulbosa (pb), pars postbulbosa (ppb), velum (vel), appendix (app), bulb length (BL), bulb width (BW), bulb ratio (BR), scolex proportions of pbo:pv:pb (SP), tentacle width (TW) and tentacle sheath width (TSW). If possible, the tentacle length (TL) was estimated. The tentacular armature was described as follows: armature homeomorphous or heteromorphous, number of hooks per half spiral row (hsr), total hook length (L) and the total length of the base of the hooks (B). The abbreviation 'nm' (not measured) indicates that no measurement was taken. All measurements are given in micrometers unless otherwise indicated. Specimens belonging to the same species from different hosts or localities were measured in the same order as cited in the material examined. If more than three measurements were taken from a single host species, the mean is given with the range in parentheses. Because tentaculariid cestodes are morphologically uniform and the genera are well defined, the species descriptions presented here are restricted to key differential features. Illustrations are provided if useful for future species identification; otherwise the reader is referred to illustrations given by other authors. The classification utilised follows Palm (1995, 1997). Host identity follows Last and Stevens (1994) for the elasmobranchs and FishBase 1998 (Froese & Pauly 1998) for the teleosts.

SYSTEMATICS

MATERIAL AND METHODS

Specimens were examined from the Australian Helminthological Collection (AHC) housed in the

A total of 19 species were identified, and 11 new locality and 20 new host records were established. Seven new species are described and

a new tentaculariid genus is erected: *Nybelinia hemipristis* sp. nov., *N. mehlhorni* sp. nov., *N. victoriae* sp. nov., *Heteronybelinia australis* sp. nov., *H. pseudorobusta* sp. nov., *Mixonybelinia cribbi* sp. nov. and *Kotorelliella jonesi* gen. et sp. nov. Detailed information on individual specimens with comments on their taxonomy and distribution are provided below.

Order TRYPANORHYNCHA Diesing, 1863

Superfamily TENTACULARIOIDEA Poche, 1926

Family TENTACULARIIDAE Poche, 1926

Genus *Nybelinia* Poche, 1926

Nybelinia aequidentata Shipley & Hornell, 1906 (Figs 1–2)

Material examined

From *Dendrochirus zebra* (Cuvier, 1829): 1 postlarva, Noumea, New Caledonia, Nov. 1997, coll. S. Pichelin (QM G 218031).

Description

SL = 7900 (Fig. 1); SW = 1775; pbo = 2975; pv = 4950; pb = 1575; vel = 925; app = 1400; BL = 1417 (1400–1450); BW = 280 (270–290); BR = 5.1:1; SP = 1.9:3.1:1. Basal tentacular swelling absent. TW basal = 100–110, TW metabasal = 110–120. Tentacle sheaths straight, TSW = 80–100, prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 2); distinctive basal armature absent. Hooks falciform, with slender shaft, stout base and strongly recurved tip, L = 57.5–65.0; B = 17.7–22.5. Hooks decrease in size towards apical region and towards base L = 35.0–57.5; B = 12.5–17.5. Smallest hook measured L = 17.5; hsr = 7–8.

Remarks

The present specimen has one of the largest scoleces among *Nybelinia* species. In addition, the postlarva is characterised by falciform hooks over 60 in length and a bulb ratio greater than 4. The postlarva is most similar to *Nybelinia aequidentata* Shipley & Hornell, 1906, described by Shipley and Hornell (1906), Pintner (1927) and

Palm (1999). Shipley and Hornell (1906) recorded the type specimen as having a scolex 4–5 mm long. The hook shape of the present specimen corresponds with those of the type, though the hooks in the present specimen are larger (57–65 compared with 49 in the type according to Shipley and Hornell (1906) or 33–38 reported by Palm (1999). Pintner (1927) redescribed the type and added information on the bulb ratio (4.3:1), hook length (48) and scolex measurements (SW = 1900, pbo = 1500, pb = 1600 and vel = 600). He also remarked that the hooks were not uniform in size but increased from the base towards the metabasal region and then decreased in the apical region of the armature. Thus, although the scolex and hook sizes of the present specimen are distinctly larger than those described from the type specimen, it has been identified as *N. aequidentata*. The present finding represents a new host and locality record.

Nybelinia syngenes Pintner, 1929 is the only other species of *Nybelinia* which has been described as having tentacular hooks with a length greater than 60 and with a similar hook form and armature pattern. However, the scolex of this species, described originally from *Sphyrna zygaena* (Linnaeus, 1758), is distinctly smaller. Whether *N. aequidentata* exhibits variation in scolex size, as described for *N. lingualis* (Cuvier, 1817) and *Heteronybelinia yamaguti* (Dollfus, 1960) (see Dollfus 1942; Palm et al. 1997; Palm 1999; Palm & Walter 2000) is not known. Palm (1999) has suggested that this might be the case for a postlarva from *Lepturacanthus savala* (Cuvier, 1829) with a scolex length of 3400, a bulb ratio of 3.3:1 and slender falciform hooks 33–38 in length.

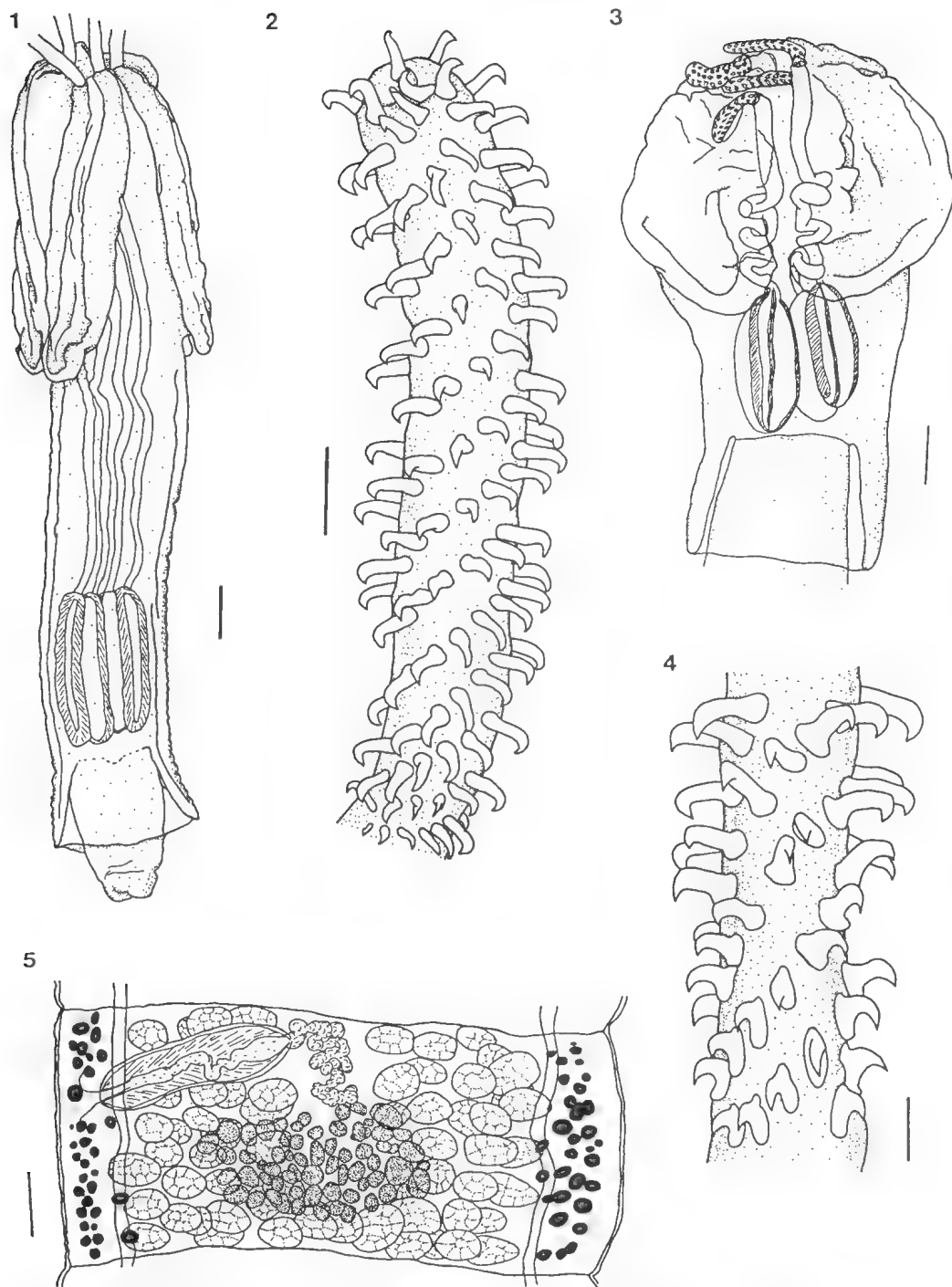
Nybelinia africana Dollfus, 1960 (Figs 3–5)

Material examined

From unidentified shark: 1 adult, Queensland, coll. J. C. Pearson (QM G 218169).

Description

SL = 1780 (Fig. 3); SW = 1134; pbo = 930; pv = 840; pb = 523; vel = 417; BL = 439 (423–459); BW = 163 (157–171); BR = 2.7:1; SP = 1.8:1.6:1. TW metabasal = 47–50. Basal tentacular swelling absent. Tentacle sheaths spirally coiled; TSW = 65–70. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles



FIGURES 1–2. *Nybelinia aequidentata* Shipley & Hornell, 1906 from *Dendrochirus zebrae*. QM G 218031. 1. Scolex. 2. Homeomorphous armature with falciform hooks. Scale bars: Figure 1, 500 μ m; Figure 2, 100 μ m. FIGURES 3–5. *Nybelinia africana* Dollfus, 1960 from an unidentified shark. QM G 218169. 3. Scolex. 4. Basal and metabasal armature. 5. Mature proglottid. Scale bars: Figure 3, 200 μ m; Figure 4, 20 μ m; Figure 5, 100 μ m.

originate in basal parts of bulbs. Tentacular armature consists of homeomorphous hooks along tentacle (Fig. 4). Tentacles not completely evaginated; metabasal armature differs distinctly from basal armature. Basal 2–3 rows of rosethorn-shaped hooks with distinct anterior extension of base, $L = 14\text{--}16$, $16\text{--}17$; metabasal hooks larger, falciform with small base, strongly recurved at tip, $L = 26\text{--}27$; $B = 10\text{--}13$. Strobila 57 mm long, with about 215 acraspedote segments which enlarge in size towards end of strobila, maximum width 1.48 mm; velum straight or very slightly scalloped; first segments $15\text{--}30 \times 600\text{--}675$, mature segments (Fig. 5) wider than long, $220\text{--}470 \times 650\text{--}970$ ($n = 4$). Pre-gravid segments (with some eggs) $440\text{--}670 \times 1150\text{--}1480$ ($n = 5$); terminal pre-gravid segment with rounded end. In mature segments, genital pore ventro-submarginal, in anterior half or anterior third of segment; genital pore to anterior end $90\text{--}150$ in mature and $180\text{--}200$ in pre-gravid segments; genital pores alternate irregularly. Cirrus sac thin-walled, elongate, $370\text{--}480 \times 70\text{--}100$ ($n = 5$), length:width ratio 4.5:1 (3.7–5.0:1), distal pole directed anteromedially, nearly reaching anterior end of proglottid, cirrus unarmed; internal and external seminal vesicle absent. Vas deferens greatly coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes of varying shape, $60\text{--}90$ in diameter, arranged in single layer centrally and in double layer peripherally; testis number $50\text{--}71$ per segment, between 5 and 8 testes anterior to cirrus ($n = 5$). Ovary follicular, in centre of segment, bilobed, each lobe $190\text{--}260 \times 140\text{--}220$, increasing in size along strobila. Vitelline follicles encircle medulla, follicles $30\text{--}50$ in diameter. Ventral and dorsal osmoregulatory canals 30 in diameter, testes extend external to ventral canal but not beyond dorsal canal.

Remarks

The present specimen closely resembles *N. africana* Dollfus, 1960 as described by Dollfus (1960) and Palm (1999) in having rosethorn-shaped basal hooks, changing to falciform metabasal hooks of similar size and shape. Additionally, the segment morphology with number and size of segments, size of cirrus sac, testes and vitelline follicles, as well as arrangement of the genital complex is similar. However, some differences were observed between the present specimen and *N. africana*. The specimen from Australia differs in having 2 to 3 rows of basal hooks with a distinct anterior extension of the base (Fig. 4), which has not been reported in other specimens of *N. africana*.

However, Dollfus (1960, figs 14, 17) illustrated comparable basal hooks, some with an anterior extension of the base. The scolex is larger in the Australian specimen (1780) compared with other material (1118–1568) (Palm et al. 1997) and the testis number is smaller. However, as most other morphological characters correspond, the specimen is identified as *N. africana* and the observed differences are considered to be due to intraspecific morphological variability. The present finding is a new locality record for the species.

Nybelinia hemipristis sp. nov.

(Figs 6–9)

Types

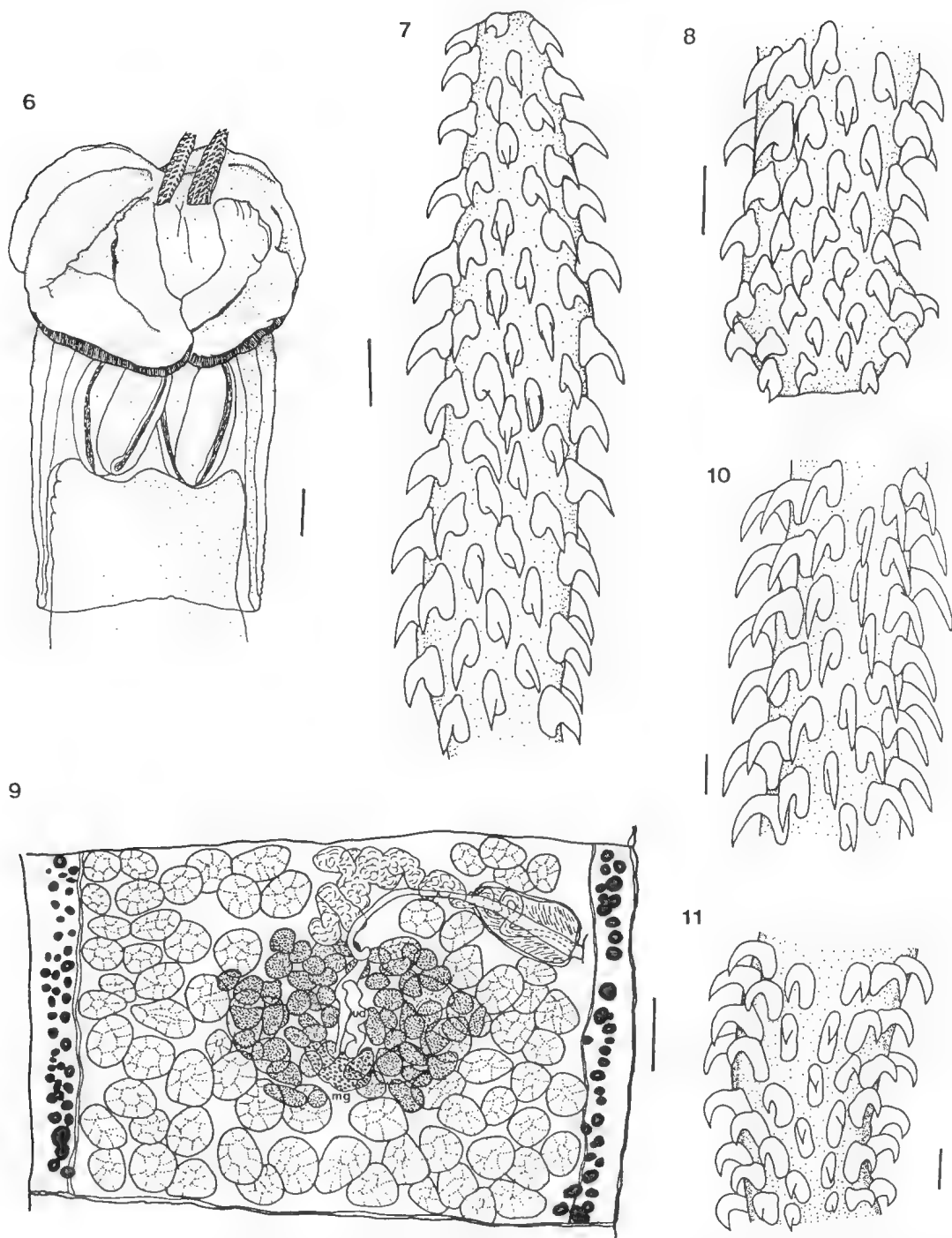
Holotype from stomach of *Hemipristis elongata* Klunzinger, 1871, Balgal, Queensland, coll. B. G. Robertson, 16.ix.1985 (SAM AHC 28309). Paratypes: 3 specimens, *Hemipristis elongatus*, Marchinbar Island, Northern Territory, coll. G. Cuthbertson, 25.v.1985 (SAM AHC 28310).

Material examined

Types.

Description

SL = 2030 (Fig. 6); SW = 1230; pbo = 1000; pv = 860; pb = 560; vel = 630; BL = 553 (550–560); BW = 218 (210–220); BR = 2.5:1; SP = 1.8:1.5:1. Tentacles short, massive, decreasing in diameter towards apical region; basal tentacular swelling absent. TW basal and metabasal = $75\text{--}85$, TW apical = $37.5\text{--}62.5$. Tentacle sheaths straight (TSW = $50\text{--}60$), prebulbar organs and muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 7); distinctive basal armature absent (Fig. 8). Hooks slender, rosethorn-shaped with anterior elongation of base, increasing in size from basal ($L = 15.5\text{--}30.0$; $B = 16.3\text{--}20.0$) towards metabasal regions ($L = 35.0\text{--}40.0$; $B = 25.0\text{--}27.5$), then decreasing in size towards apical ($L = 27.5\text{--}32.5$; $B = 15.0\text{--}20.0$) region; hsr = 6. Strobila acraspedote, velum straight; 33 mm long, maximum width 1030, number of segments 300. Mature segments (Fig. 9) wider than long, $600\text{--}670 \times 750\text{--}920$. Genital pore submarginal, 200 from anterior end, alternating irregularly. Cirrus sac short and stout, $180\text{--}210 \times 50\text{--}100$ ($n = 5$), length:width ratio 2.9:1 (2.0–3.6:1), distal pole directed



FIGURES 6–9. *Nybelinia hemipristis* sp. nov. from *Hemipristis elongata*. Holotype, SAM AHC 28309. 6. Scolex. 7. Metabasal armature. 8. Basal armature. 9. Mature proglottid. Note short cirrus sac, the uterine duct (ud), and the Mehlis' gland (mg). Scale bars: Figure 6, 200 μ m; Figures 7–8, 40 μ m; Figure 9, 100 μ m. FIGURES 10–11. *Nybelinia jayapaulazariahi* Reimer, 1980 from a 'sole'. QM G 207318. 10. Metabasal armature. 11. Basal armature. Scale bars: Figures 10–11, 10 μ m.

anteromedially, not reaching anterior end of segments, cirrus unarmed; internal and external seminal vesicle absent. Vas deferens coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes 84–97 in number, 55–85 in diameter centrally and 40–60 peripherally, distributed in single layer; arranged in 2 lateral groups, confluent posterior to ovary; extend between ovarian lobes, about 6–7 testes anterior to cirrus sac. Ovary in centre of segment, ovarian lobes 200–260 x 120–160. Vagina ventral to cirrus sac. Vitelline follicles encircle medulla; follicles 25–40 in diameter.

Remarks

The present specimens, with rosethorn-shaped hooks diminishing in size towards the apical armature and a strobila consisting of acraspedote segments, resemble *N. anthicosum* Heinz & Dailey, 1974. However, the species differ in having different scolex forms, tentacles, tentacular armatures and sizes. *N. anthicosum* has an elongated prominent velum, long tentacles and tentacular hooks which are distinctly spaced (see Heinz & Dailey 1974). The largest hooks occur in the 7th to 9th rows. *N. hemipristis* sp. nov. has a massive scolex with a shorter velum (Fig. 6), short tentacles and tentacular hooks which are tightly spaced along the tentacle. The largest hooks are in the 10th to 14th rows. In the last few hook rows, the size and number of hooks per half spiral row decrease rapidly (Fig. 7). In *N. anthicosum* the hook size diminishes gradually towards the apical part of the tentacle. As with *N. anthicosum*, *N. hemipristis* is a species without a characteristic basal armature and with a smaller basal than metabasal hook size, therefore belonging to species subgroup 'Aa' of Palm (1999).

The description of the strobilar characters of *N. hemipristis* demonstrates that this species has a very characteristic, short, stout cirrus sac, with a length:width ratio of 2 in some segments, a feature unusual in most species of *Nybelinia*. However, this character might prove to be of taxonomic significance in the future.

The new species is named after the elasmobranch host genus, *Hemipristis*.

Nybelinia jayapaulazariahi Reimer, 1980
(Figs. 10–11)

Material examined

From 'sole', either *Synaptura nigra* Macleay, 1880 or *Aseraggodes macleayanus* (Ramsay,

1881): 1 postlarva, Moreton Bay, Queensland, coll. J. C. Pearson, 1968 (QM G 207318).

Description

SL = 1060; SW = 700; pbo = 470; pv = 450; pb = 365; BL = 323 (320–325); BW = 119 (85–135); BR = 2.7:1; SP = 1.3:1.2:1. TW = 32.5–35; hsr = 6. Basal tentacular swelling absent. Retractor muscles originate in basal parts of bulbs. Tentacular armature consists of homeomorphous slender uncinuate hooks, L = 15.0–16.3, B = 11.2–13.7 (Fig. 10). Size of hooks diminishes towards basal part of tentacle, L = 11.2–13.7, B = 8.7–11.2 (Fig. 11).

Remarks

N. jayapaulazariahi was originally described from *Cynoglossus* sp. from the Bay of Bengal, India by Reimer (1980). Palm (1999) redescribed the species from another host, *Harpodon nehereus* (Hamilton-Buchanan, 1822), also from India. The tentacular armature has characteristic, slender, regularly curved hooks which increase in size towards the metabasal part of the tentacle. The present specimen, also from a 'sole', has a similar hook shape (compare Fig. 4 with Fig. 5 of Palm 1999) and bulb ratio, while it differs in having a larger scolex (1060 in the present specimen compared with 530 described previously) and hook size (11.2–16.3 in the current specimen compared with 5.6–11.2 in previous descriptions). However, the present specimen was in a poor state of preservation, and the larger scolex might be related to the slightly larger hook size. A small scolex of about 0.5–1.0 mm, together with the uncinuate hook form, is characteristic for *N. jayapaulazariahi*, and soles seem to be important intermediate hosts. The present finding represents a new locality record for the species.

Nybelinia mehlhorni sp. nov.
(Figs 12–14)

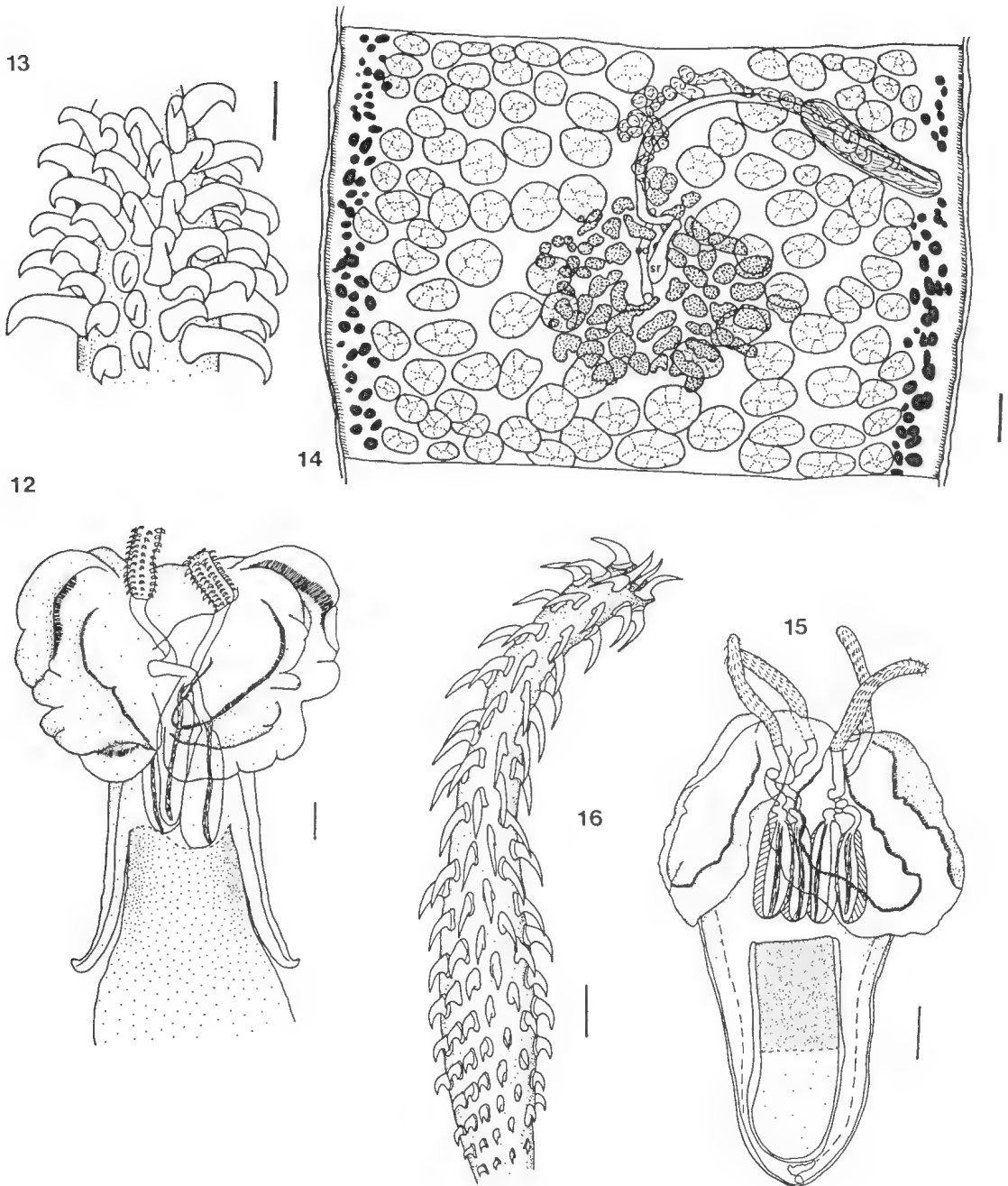
Types

Holotype from stomach of *Hemigaleus microstoma* Bleeker, 1852, Heron Island, Queensland, coll. P. McBoarman, 20.xii.1995 (QM G 218032); paratype, same data (QM G 218033).

Material examined
Types.

Description

SL = 560 (Fig. 12); SW = 400; pbo = 330;



FIGURES 12–14. *Nybelinia mehlhorni* sp. nov. from *Hemigaleus microstoma*. Types, QM G 218032–3. 12. Scolex. 13. Metabasal and apical armature. 14. Mature proglottid. Note the uterine duct (ud) and the seminal receptacle (sr). Scale bars: Figure 12, 50 μ m; Figure 13, 10 μ m; Figure 14, 50 μ m. FIGURES 15–16. *Nybelinia scoliodoni* (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) from *Diodon hystrix*. QM G 218035–7. 15. Scolex. 16. Basal and metabasal armature, external surface. Scale bars: Figure 15, 150 μ m; Figure 16, 25 μ m.

pv = 125; pb = 250; vel = 200; BL = 178 (150–200); BW = 58 (50–70); BR = 3.1:1; SP = 1.3:0.5:1. Tentacles short; basal tentacular swelling absent; TW = 22.5–27.5. Tentacle sheaths sinuous to spirally coiled (TSW = 17.5–20.0); muscular rings around basal part of tentacle sheaths seen. Retractor muscles originate in basal parts of bulbs. Tentacular armature homeoacanthous, homeomorphous (Fig. 13); distinctive basal armature absent. Hooks falciform, with stout base, elongated handle and strongly recurved tip. Hooks increase in size from basal (L = 3.5–7.5, B = 2.5–5.0) to metabasal region (L = 15.0–17.5, B = 6.3–8.7) then decrease towards apex (L = 11.3–13.8, B = 2.5–4.3); hsr = 7. Small worms, length 25 (16) mm, maximum width 950 (700) with 135 (90) segments. Strobila acraspedote, velum straight; pre-mature (testes visible) proglottids (Fig. 14) 80–280 long x 560–790 wide; mature segments (female genitalia developed) wider than long, 380–600 x 600–900; terminal segment 830 x 800. Genital pore almost lateral, 130–200 from anterior end (190 in terminal segment); pores alternate irregularly. Cirrus sac elongate, 170–220 x 40–60 (n = 5) in mature segments, length:width ratio 4.1:1 (2.8–5.5:1), distal pole directed anteromedially, not reaching anterior end of segments; cirrus unarmed, internal and external seminal vesicles absent. Vas deferens greatly coiled in midline of segments, extending posteriorly towards female genital complex. Testes 103–120 in number, 80 x 95 in size, smaller testes peripheral, 35–40 in size, distributed in single layer; testes in 2 lateral groups confluent posterior to ovary; 10–16 testes anterior to cirrus sac. Vagina tubiform, 30 in diameter, ventral to cirrus sac, passes anteromedially to midline, then posteriorly to ovary; seminal receptacle present, 60–90 x 25–50. Ovary in centre of segment, ovarian lobes 250–300 x 160–210. Vitelline follicles encircle medulla, follicles 30–45 in diameter. Uterine pore absent.

Remarks

Following Palm (1999), *N. mehlhorni* sp. nov. belongs to *Nybelinia* species without a characteristic basal armature and a basal hook size smaller than the metabasal one, thus belonging to the subgroup 'Aa'.

On the basis of the hook shape, the species resembles *N. aequidentata* (Shipley & Hornell, 1906) and *N. goreensis* Dollfus, 1960. While the former is much larger than the present specimen,

the latter species has different scolex proportions as well as a different hook arrangement, as illustrated recently by Palm and Walter (2000).

N. mehlhorni sp. nov. also resembles *N. bengalensis* Reimer, 1980 in its falciform hooks and in hook size (Reimer 1980). However, *N. bengalensis* can be distinguished by having a distinctly different scolex form and size, a bulb ratio of about 2, long and slender tentacle sheaths and tentacles with spaced falciform hooks (Reimer 1980). By contrast, *N. mehlhorni* sp. nov. has short tentacles with hooks tightly spaced along the tentacle. The scolex (0.56 mm in total length) is much smaller.

The new species is named in honour of Prof. Heinz Mehlhorn, Heinrich-Heine-University, Düsseldorf.

Nybelinia schmidtii Palm, 1999

Material examined

From *Isurus oxyrinchus* Rafinesque, 1810: 1 adult, Bicheno, Tasmania, coll. B. G. Robertson, 24.iv.1987 (SAM AHC 28313).

Description

SL = 1600; SW = 850; pbo = 1040; pv = 680; pb = 340; vel = 600; BL = 298 (270–330); BW = 131 (110–150); BR = 2.3:1; SP = 3.0:2.0:1. TW basal = 45–48, TW metabasal = 30.0–32.5; hsr = 5–6. Basal tentacular swelling absent. Tentacle sheaths spirally coiled, TSW = 25–40. Prebulbar organs absent, muscular rings present around the tentacle sheaths. Retractor muscles originate in basal part of bulbs. Tentacular armature homeoacanthous, homeomorphous, consisting of massive rosethorn-shaped hooks with anterior extension of base, size in metabasal region L = 13.8–15.0, B = 11.3–12.5, decreasing towards base, L = 8.8–11.3, B = 6.2–8.8. Characteristic basal armature absent. Strobila immature with few segments, acraspedote; segments wider than long (660–690 x 15–60).

Remarks

The present specimen closely resembles that of the type, also from *Isurus oxyrinchus* (syn. *Isurus glaucus*), in having similar scolex proportions and almost identical hook sizes. Other species with a similar tentacular armature are *Nybelinia strongyla* Dollfus, 1960 and *Heteronybelinia australis* sp. nov. (*vide infra*). While the latter species differs in having homeomorphous hooks of different sizes on the

internal and external tentacle surfaces as well as smaller basal hooks, *N. strongyla* differs in scolex proportions and larger hook sizes. The present record extends the range of distribution from the South African to the southern Australian coast.

Nybelinia scoliodoni (Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) (Figs 15–16)

Material examined

From *Diodon hystrix* Linnaeus, 1758: Heron Island, Queensland, 2 postlarvae, coll. J. Sakanari, 23.viii.1986 (QM G 218034); 8 postlarvae, coll. M. K. Jones, 6.vii.1995 (QM G 218035–218037); 8 postlarvae, coll. T. H. Cribb, Jan. 1997 (QM G 218038–218041).

From *Makaira indica* (Cuvier, 1832): 1 postlarva, Cape Bowling Green, Queensland, coll. P. Speare, 18.ix.1987 (SAM AHC 21351).

From *Istiophorus platypterus* (Shaw & Nodder, 1792): Whitsunday Island, Queensland, coll. P. Speare, 5.xii.1988 (SAM AHC 21351).

From *Carcharhinus limbatus* (Valenciennes, 1839): 1 adult, stomach, Bremer Island, Northern Territory, coll. J. Stevens, 29.v.1985 (SAM AHC 28314).

Description

SL = 1350, 1115 (Fig. 15); SW = 860, 800; pbo = 670, 520; pv = 230, 210; pb = 300, 320; vel = 330, 330; app = 310, 200; BL = 288 (280–300), 282 (260–300); BW = 115 (110–120), 125 (120–130); BR = 2.5:1, 2.3:1; SP = 2.2:0.8:1, 1.6:0.7:1. Tentacles nearly completely evaginated, TL = 390, 375; basal tentacular swelling absent. TW at basal armature 35, 30; TW at metabasal armature 50, 45; TW at apex 30, 25. Tentacle sheaths sinuous, TSW = 30, 40; prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal parts of bulbs. Metabasal armature homeoacanthous, homeomorphous; distinctive basal armature present (Fig. 16). Basal armature consists of about 10 rows with compact rosethorn-shaped hooks, increasing in size from L = 4.5, B = 3.9 (row 1) to L = 19.5, B = 11.7 (row 10). From row 11, hook form changes to slender spiniform, L = 22.7, B = 13.0. Metabasal and apical hooks L = 29.9, with small base, B = 11. Number of hooks per half row (hsr) 6–7 in basal region, decreasing to 5 in metabasal and apical regions.

Remarks

Nybelinia scoliodoni is a widely distributed tentaculicid and is here recorded for the first time from Australian waters. The species is easily recognised by its rosethorn-shaped basal armature of about 11 rows which is followed by long, spiniform metabasal hooks. The present specimens correspond with the description given by Palm (1999) in having a similar armature and bulb ratio. They differ in having a larger scolex and hook size. However, they correspond closely to the original description of *Nybelinia* (= *Tentaculicid*) *scoliodoni* of Vijayalakshmi et al. (1996). The present findings constitute three new host records. *C. limbatus* has been recorded previously as a definitive host for *N. scoliodoni* by Palm (1999). The specimens described here are the same as those reported by Speare (1999).

Nybelinia strongyla Dollfus, 1960 (Figs 17–20)

Material examined

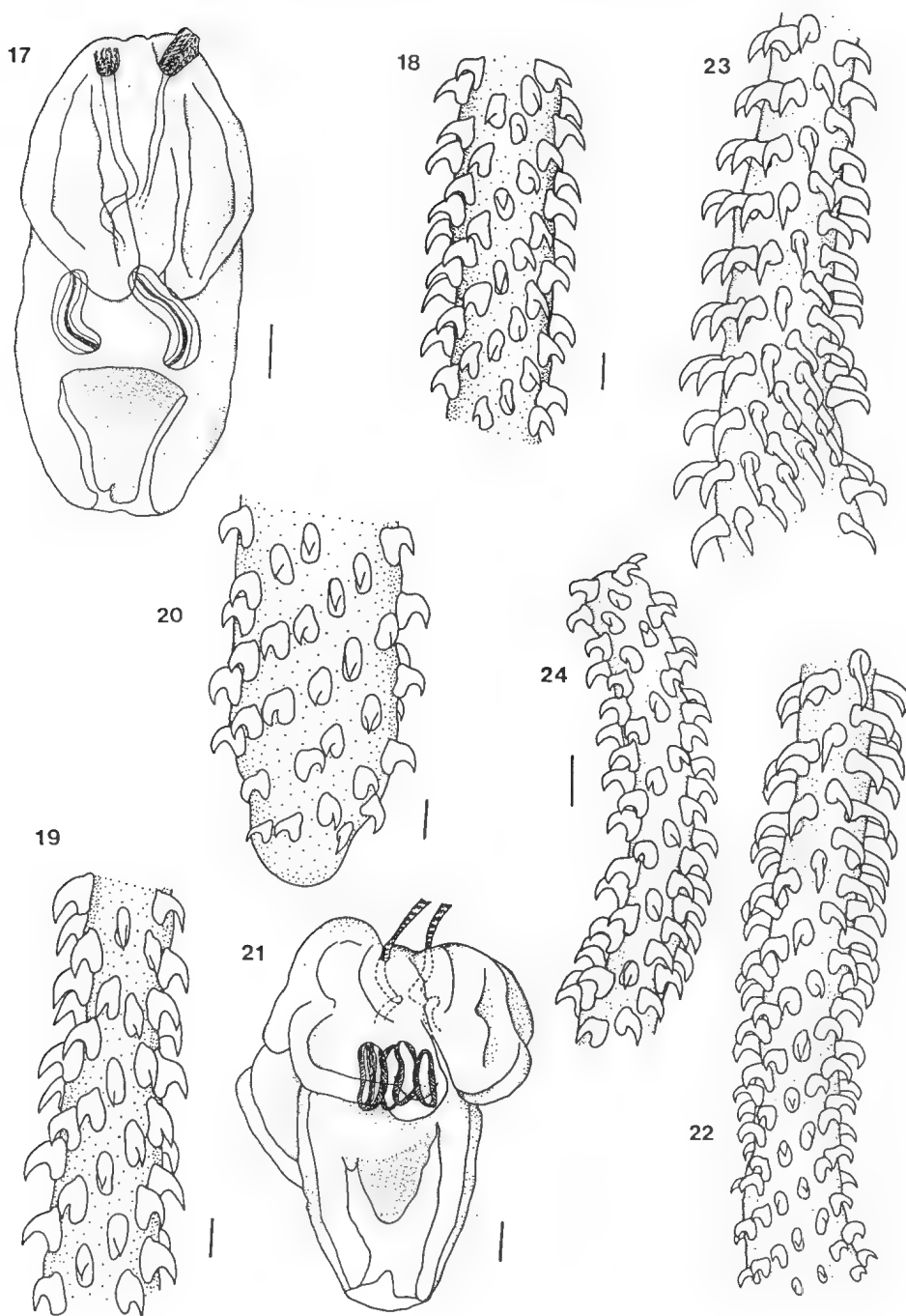
From *Argyrosomus hololepidotus* Lacépède, 1802: 2 postlarvae from stomach, Murray Mouth, South Australia, coll. M. G. O'Callaghan, May 1992 (SAM AHC 28345).

From *Johnius vogleri* (Bleeker, 1853): 1 postlarva from body cavity, Heron Island, Queensland, coll. J. Reddich, Jan 1997 (QM G 218109).

Description

Postlarvae from *A. hololepidotus*: SL = 1303, 1566 (Fig. 17); SW = 648, 796; pbo = 700, 781; pv = 647, 764; pb = 292, 355; vel = 332, 326; app = 374, 429; BL = 286 (244–292), 355 (334–380); BW = 86 (82–90), 98 (92–107); BR = 3.3:1, 3.6:1; SP = 2.4:2.2:1, 2.2:2.2:1. Tentacles not completely evaginated; basal tentacle swelling absent. TW = 50–58, 43–45. Tentacle sheaths sinuous, TSW = 36–40, 36–40; prebulbar organs and muscular rings around basal part of tentacle sheaths not visible. Retractor muscles originate in basal part of bulbs. Tentacle armature homeoacanthous, homeomorphous (Fig. 18); distinctive basal armature absent. Hooks slender, rosethorn-shaped, increasing in size from basal towards metabasal part of tentacle. Metabasal hooks L = 17.5–20.0; B = 13.8–16.3; basal hooks L = 10.0–12.5; B = 10.0–12.5; hsr = 7.

Postlarva from *J. vogleri*: SL = 1880; SW = 1660; pv = 680; pb = 440; BL = 308 (300–325); BW = 129 (115–150); BR = 2.4:1;



FIGURES 17–18. *Nybelinia strongyla* Dollfus, 1960 from *Argyrosomus hololepidotus*. SAM AHC 28345. 17. Scolex. 18. Metabasal armature. Scale bars: Figure 17, 150 μ m; Figure 18: 15 μ m. FIGURES 19–20. *Nybelinia strongyla* from *Johniops vogleri*. QM G218109. 19. Metabasal armature. 20. Basal armature. Scale bars: Figure 19–20: 10 μ m. FIGURES 21–24. *Nybelinia thyrstites* Korotaeva, 1971 from *Trachurus declivis*. QM G 214194–5. 21. Scolex. 22. Basal armature. 23. Metabasal armature with falciform hooks. 24. Apical armature with rosethorn-shaped hooks. Scale bars: Figure 21, 200 μ m; Figures 22–24, 25 μ m.

SP = $-:1.5:1$. TW basal = 37–40, TW metabasal = 30–33. Basal tentacular swelling absent. Tentacle sheaths straight; TSW = 20–25. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths absent. Retractor muscles originate in basal part of bulbs. Armature homeoacanthous, homeomorphous (Fig. 19); characteristic basal armature absent (Fig. 20). Hooks rosethorn-shaped with anterior extension of basal plate; hooks in basal part of tentacle smaller ($L = 7.5\text{--}10.0$; $B = 7.5\text{--}9.5$) than in metabasal ($L = 13.8\text{--}16.3$; $B = 10.0\text{--}12.5$) armature. Number of hooks per half spiral (hsr) diminishes from 6–7 in metabasal region to 5–6 in apical part of tentacle.

Remarks

Nybelinia strongyla Dollfus, 1960 was described from a postlarva from the west coast of Africa, and is characterised by the homeoacanthous tentacular armature with slender rosethorn-shaped hooks, reaching a size of up to 16 in the metabasal armature. Palm and Walter (2000) described adult specimens of *N. strongyla* from Africa. The present specimens correspond closely in their tentacular armature as well as in scolex proportions to those specimens described by Dollfus (1960) and Palm and Walter (2000). Minor variations in the hook pattern are observed within *N. strongyla* but are difficult to define, and many scolex characters within tentaculariids appear to be variable (Palm 1999, Palm and Walter 2000). Therefore, the postlarvae described above are identified as *N. strongyla*. However, some doubt surrounding the identification remains. Further studies are needed to determine whether postlarvae with rosethorn-shaped hooks as described above are conspecific with the African material, or whether they belong to a new species of *Nybelinia*. *Argyrosomus hololepidotus* is a new host record, and the distribution of the species is extended to the southern Australian coast.

The specimen from *J. vogleri*, with rosethorn-shaped hooks, resembles *N. lingualis*, *N. schmidtii*, *N. sphyrnae*, *N. strongyla* and *N. thyrssites*. It differs from *N. lingualis* in having basal hooks with an anterior extension of the basal plate, and from *N. thyrssites* in having differently shaped metabasal hooks and a larger bulb ratio (see below). *N. schmidtii* differs in having smaller hooks and different scolex proportions. *N. sphyrnae* differs in having slender, more uncinat hooks in the metabasal armature, while the hooks are more massive rosethorn-shaped in *N.*

strongyla. In the present specimen, the basal hook length is slightly smaller than described by Palm and Walter (2000) for *N. strongyla*. However, the metabasal hooks are the same size. Although the scolex proportions were difficult to measure in the present specimen, it is also identified as *N. strongyla*, representing a new host and locality record.

Nybelinia thyrssites Korotaeva, 1971
(Figs 21–24)

Material examined

From *Trachurus declivis* Jenyns, 1841: 2 postlarvae from stomach wall, Crayfish Bay, Tasmania, coll. K. B. Sewell, 11.v.1987 (QM G 214194, 212145).

From *Carcharhinus brachyurus* (Günther, 1870): 1 adult from stomach, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28312).

From *Mustelus antarcticus* Günther, 1870: 1 adult from stomach, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28311).

Description

SL = 2032, 1550 (Fig. 21); SW = 1520, 700; pbo = 1024, 610; pv = 640, 500; pb = 368, 520; vel = 992, 490; app = 496; BL = 358 (355–365), 495 (490–500); BW = 117 (114–120), 155 (140–170); BR = 3.1:1, 3.2:1; SP = 2.8:1.7:1, 1.2:1:1. Tentacle sheaths spirally coiled; TSW = 51–57, 35–45. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths present. Retractor muscles originate in basal part of bulbs. Tentacles long (TL = 832) and slender, basal tentacular swelling absent; TW basal = 38–44, 25–30; TW metabasal = 57.0, 57.7–62.5; TW apical 32.0, 27.5. Characteristic basal armature present (Fig. 22), consisting of about 7–8 rows of homeomorphous, rosethorn-shaped hooks with slight anterior extension, increasing in size towards metabasal armature (1st row hooks: $L = 9.5\text{--}11.0$, $B = 8.0\text{--}11.0$, $L = 7.5\text{--}8.7$, $B = 6.3\text{--}7.5$; 8th row: $L = 15.8\text{--}17.4$, $L = 16.2\text{--}17.5$, $B = 11.0\text{--}12.6$, $B = 10.0\text{--}12.5$). Metabasal armature of about 12–14 rows of hooks, with largest hooks in rows 12–17. Metabasal armature with slender falcate to falciform hooks ($L = 21.7\text{--}26.9$, $B = 8.7\text{--}11.0$; $L = 21.3\text{--}24.0$, $B = 11.3\text{--}12.5$) (Fig. 23). Apical hooks rosethorn-shaped, with hook form changing from slender rosethorn-shaped with slight anterior extension to rosethorn-shaped with distinct anterior extension (Fig. 24).

Hooks diminish in size towards apical region (34th row of hooks: L = 14.2–15.8, B = 11.0–14.2); hsr basal: 6–7; hsr metabasal and apical: 6.

Remarks

N. thyrsites was redescribed in detail by Beveridge and Campbell (1996). The present material corresponds with the redescription given. In addition, the basal hook form differs from the metabasal and apical hooks; thus, the species belongs to subgroup 'Ba' of Palm (1999). The present specimens from *Trachurus declivis* provide a further example in which the postlarvae can be larger than adult worms, and also show variable scolex measurements depending on the state of contraction. *Trachurus declivis* and *Carcharhinus brachyurus* are new hosts for *N. thyrsites*.

Nybelinia victoriae sp. nov.

(Figs 25–26)

Types

Holotype from body cavity of *Lepidotrigla modesta* Waite, 1899, Port Phillip Bay, Victoria, coll. R. Norman, 17.iii.1989 (SAM AHC 28343); paratype, same data (SAM AHC 28344).

Material examined

Types.

Description

SL = 1030, 1050 (Fig 25); SW = 700, 650; Pbo = 570, 450; Pv = 350, 320; Pb = 315, 320; BL = 310 (300–315), 310 (305–320); BW = 124 (115–135), 116 (110–125); BR = 2.5:1, 2.7:1; SP = 1.8:1.1:1, 1.4:1.0:1. Tentacles elongate; basal tentacular swelling absent. TW = 40.0–50.0, 45.0–50.0. Tentacle sheaths sinuous to spirally coiled (TSW = 40.0–50.0, 35.0–40.0); prebulbar organs and muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal part of bulbs. Armature homeoacanthous, homeomorphous (Fig. 26); distinctive basal armature absent. Hooks falciform, with stout base, elongated handle and strongly recurved tip. Hooks increase in size from basal (L = 7.5–10.0, B = 6.3–8.8) to metabasal region (L = 12.5–15.0, B = 7.0–8.0) and decrease towards apical (L = 11.3–12.5, B = 6.3–8.0) part of tentacle; hsr = 7.

Remarks

This species, with a tentacular armature

consisting of slender falciform hooks, increasing in size towards the metabasal region and decreasing in size towards the apical region, resembles *Nybelinia aequidentata* Shipley & Hornell, 1906; *N. syngenes* Pintner, 1927; *N. anantaramanorum* Reimer, 1980; and *N. bengalensis* Reimer, 1980. While the former two species differ in having different scolex proportions and distinctly larger hooks (see remarks on *N. aequidentata*), the present specimens are most similar to *N. bengalensis* and *N. anantaramanorum*. *N. anantaramanorum* has larger hooks and was considered a *species inquirenda* by Palm and Walter (2000). *N. bengalensis* differs in having different scolex proportions, including very short bulbs (BR < 2) (Reimer 1980). Thus, the present specimens represent a new species here named *Nybelinia victoriae* sp. nov., the specific epithet being derived from the Australian state from which samples were collected. With hook size smaller in the basal rather than the metabasal region, the species is considered to belong to subgroup 'Aa' of Palm (1999).

Genus *Heteronybelinia* Palm, 1999

Heteronybelinia australis sp. nov.

(Figs 27–30)

Types

Holotype from stomach of *Carcharhinus amboinensis* (Müller & Henle, 1839), St Lawrence, Queensland, coll. B. G. Robertson, 29.x.1985 (SAM AHC 28315); paratype, same data (SAM AHC 28316).

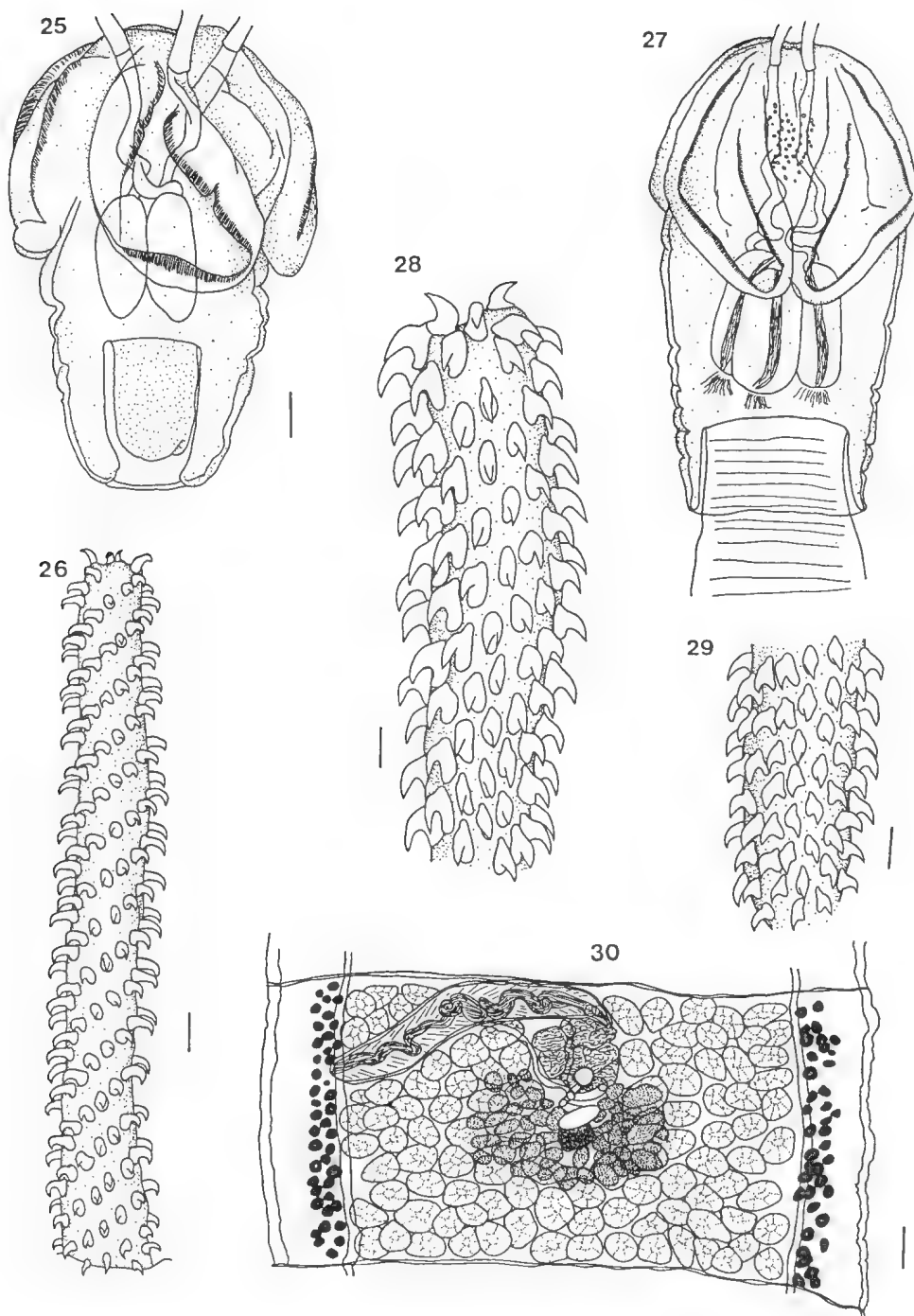
Material examined

From *Carcharhinus amboinensis*: types.

From *Carcharhinus brachyurus*: 1 specimen, Goolwa, South Australia, coll. R. Martin, 28.x.1985 (SAM AHC 28317).

Description

SL = 1190, 1210 (Fig. 27); SW = 660, 680; pbo = 650, 700; pv = 530, 650; pb = 350, 310; vel = 220, 190; BL = 313 (305–320), 308 (290–340); BW = 138 (125–150), 119 (110–130); BR = 2.3:1, 2.6:1; SP = 1.9:1.7:1, 2.3:2.1:1. Tentacle sheaths spirally coiled. TSW = 27.5–32.5, 25.0–35.0. Tentacles robust, TL = 255–290, increasing in width towards apex. TW basal and metabasal 30.0–32.5; basal tentacular swelling absent. Prebulbar organs absent; muscular rings



FIGURES 25–26. *Nybelinia victoriae* sp. nov. from *Lepidotrigla modesta*. Types, SAM AHC 28343–4. 25. Scolex. 26. Basal and metabasal armature. Scale bars: Figure 25, 100 μ m; Figure 26, 20 μ m. FIGURES 27–30. *Heteronybelinia australis* sp. nov. from *Carcharhinus amboinensis*. Types, SAM AHC 28315–6. 27. Scolex. 28. Metabasal armature. 29. Basal armature. 30. Mature proglottid. Note the uterine pore. Scale bars: Figure 27, 100 μ m; Figures 28–29, 10 μ m; Figure 30, 50 μ m.

around basal parts of tentacle sheaths present. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, with hooks tightly spaced along tentacle (Fig. 28); characteristic basal armature absent (Fig. 29). Hooks massive, rose-thorn shaped, with slight anterior extension of base, increase in size from basal towards metabasal armature. Hook size differs on bothridial/antibothridial ($L = 12.5\text{--}15.0$, $B = 11.3\text{--}13.7$) and antibothridial/bothridial ($L = 11.3\text{--}12.5$, $B = 7.0\text{--}8.7$) tentacle surfaces (Fig. 28), with two tentacles having largest hooks on bothridial surfaces and two other tentacles having largest hooks on antibothridial surfaces. Basal hooks $L = 5.0\text{--}7.5$, $7.5\text{--}8.7$; $B = 8.7\text{--}10.0$ (internal) and $L = 5.0\text{--}6.3$, $5.0\text{--}7.5$; $B = 3.8\text{--}5.0$, $5.0\text{--}6.3$ (external); $h\text{sr} = 6\text{--}7$. Strobila only very slightly craspedote, velum scalloped; total length 18.0 and 15.0 mm, maximum width 640 and 730, with 125 and 155 segments. In holotype, terminal segment premature (320×550), segments wider than long, 231×630 . Genital pores ventro-submarginal, 60 from anterior margin; alternate irregularly. Cirrus sac of pre-mature segments elongate and slender, $210\text{--}230 \times 35\text{--}50$ ($n = 5$), length:width ratio 5.3:1 (4.6–6.0:1), with distal pole directed anteromedially, reaching anterior end of segment (Fig. 30); cirrus unarmed; internal and external seminal vesicles absent. Vas deferens coiled, extends posteriorly from cirrus sac towards female genital complex. Testes 106–130 in number, smallest testes at margin of medulla, distributed in 1–2 layers; in 2 lateral groups, confluent posterior to ovary; extend between ovarian lobes; 8–10 testes anterior to cirrus sac. Ventral osmoregulatory canal 15 in diameter, internal to sinuous dorsal canal, 5 in diameter; 24 prominent bands of longitudinal muscles on each side of strobila. Segments in paratype mature, wider than long (240×700 to 380×720). Genital pores 110 from anterior margin. Cirrus sac of mature segments (Fig. 30) elongate and slender, $260\text{--}320 \times 50\text{--}60$ ($n = 5$), length:width ratio 5.2:1 (4.3–5.8:1). Central testes 45–65 in diameter, smallest testes peripheral, 30–50 in diameter, distributed in 1–2 layers; ovarian lobes $110\text{--}200 \times 80\text{--}110$, seminal receptacle $50\text{--}65 \times 25\text{--}30$.

Remarks

Heteronybelinia australis sp. nov. has a unique armature. The tentacular hooks are tightly spaced and appear homeomorphous along the tentacle. However, the hook sizes differ on the bothridial and antibothridial tentacular surfaces. In addition,

two tentacles have the largest hooks on the bothridial surfaces while the other two tentacles have the largest hooks on the antibothridial surfaces. Whether this armature pattern is unique or whether it occurs in other tentaculariid species remains to be determined.

The specific epithet indicates the occurrence of the species in Australian waters.

Heteronybelinia estigmaena (Dollfus, 1960)
(Figs 31–36)

Material examined

From *Carcharhinus limbatus* Valenciennes, 1839: 16 adults from spiral valve, Geraldton, Western Australia, coll. B. G. Robertson, 27.xi.1986 (SAM AHC 21352, 28318); 4 adults from spiral valve, Nickol Bay, Western Australia, coll. B. G. Robertson, 11.xi.1986 (SAM AHC 28319); 3 adults from spiral valve, Darwin Harbour, Northern Territory, coll. B. G. Robertson, 28.viii.1986 (SAM AHC 28320); 6 adults from spiral valve, Fog Bay, Northern Territory, coll. B. G. Robertson, 4.x.1986 (SAM AHC 28329).

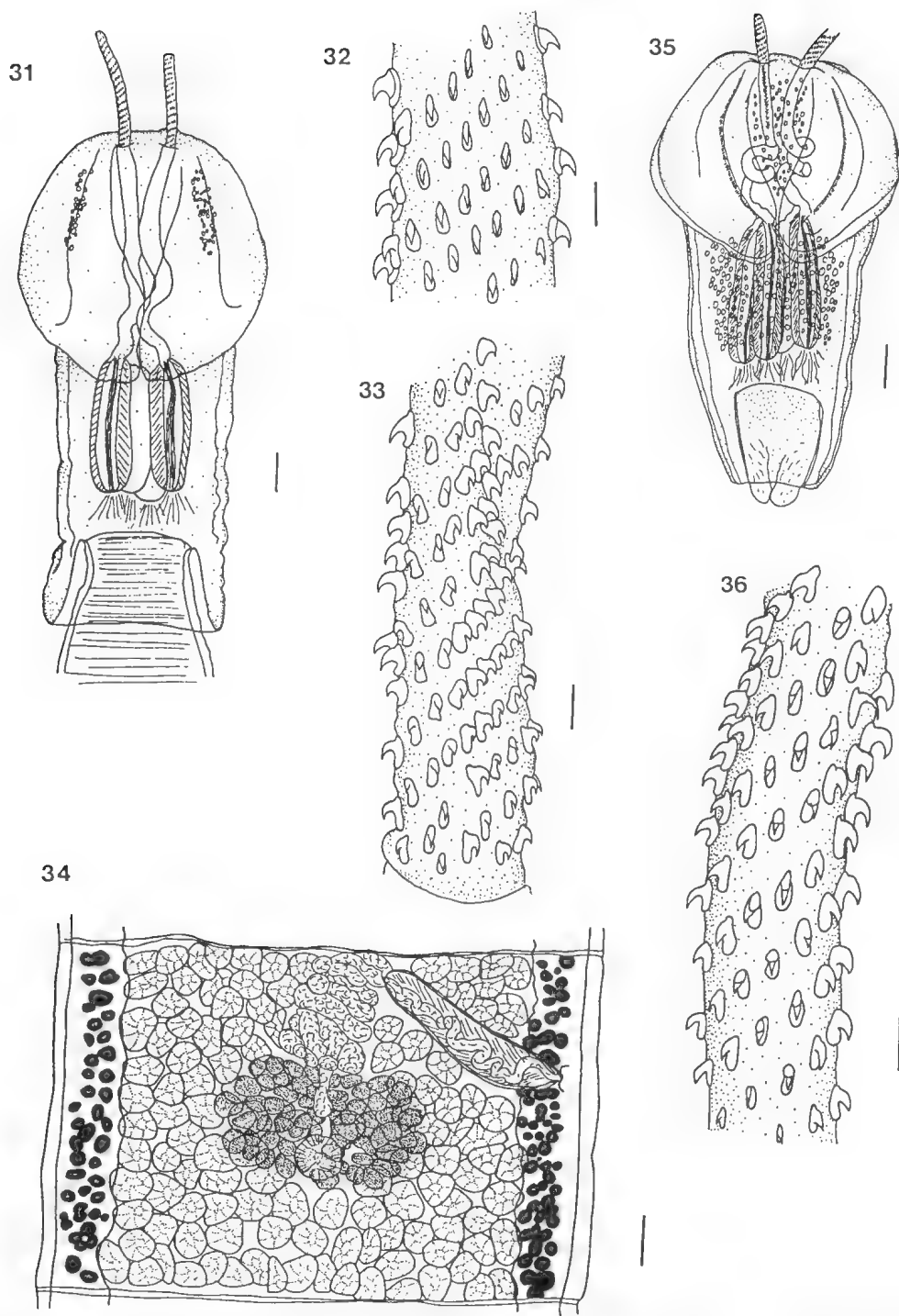
From *Carcharhinus amblyrhynchoides* (Whitley, 1934): 2 adults from spiral valve, Tommy Cut Mouth, Northern Territory, coll. B. G. Robertson, 10.ix.1986 (SAM AHC 28321).

From *Carcharhinus* sp: 3 adults from spiral valve, Queensland, coll. B. G. Robertson, Oct. 1985 (SAM AHC 18322).

From *Sarda australis* (Macleay, 1881): 9 postlarvae from gill arches, Heron Island, Queensland, coll. M. K. Jones, Jan. 1991 (QM G 218042–218046).

Description

Adult: $SL = 1650$, 1500 (Fig. 31); $SW = 790$, 770 ; $pbo = 820$, 820 ; $pv = 690$, 610 ; $pb = 480$, 430 ; $ppb = 110$, 80 ; $vel = 330$, 320 ; $BL = 455$ ($440\text{--}480$), 425 ($420\text{--}430$); $BW = 133$ ($130\text{--}140$), 120 ($118\text{--}122$); $BR = 3.4:1$, $3.6:1$; $SP = 1.7:1.4:1$, $1.9:1.4:1$. Tentacles long, slender ($TL = 520$, 560), $TSW = 42.5\text{--}47.5$, $45.0\text{--}55.0$; TW basal $45\text{--}50$, $42.5\text{--}45$; TW apical $25\text{--}30$, $27.5\text{--}32.5$; basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths visible in one specimen. Retractor muscles originate at bases of bulbs. Tentacular armature homeoacanthous, heteromorphous, no characteristic basal armature present (Figs 32–33). Hooks rosethorn-shaped, increase in size towards metabasal part of



FIGURES 31–34. *Heteronybelinia estigmae* (Dollfus, 1960) from *Carcharhinus limbatus*. SAM AHC 28318–20. 31. Scolex. 32. Metabasal armature. 33. Basal armature. 34. Mature proglottid. Scale bars: Figure 31, 150 μ m; Figures 32–33, 15 μ m; Figure 34, 100 μ m. FIGURES 35–36. *H. estigmae* from *Sarda australis*. QM G 218042–46. 35. Scolex. 36. Basal armature. Scale bars: Figure 35, 150 μ m; Figure 36, 15 μ m.

tentacle. Hook form varies from compact and rosethorn-shaped (bothridial) to smaller rosethorn-shaped hooks with elongated base (antibothridial). Hook size, metabasal, $L = 11.3\text{--}12.5$; $B = 9.3\text{--}10.8$ (bothridial) and $L = 9.3\text{--}10.8$; $B = 10$ (antibothridial), with largest hooks $L = 13.8\text{--}15.0$; $B = 10.0\text{--}12.5$ (bothridial); hooks diminish in size towards apical part of tentacle. Hook size in basal region $L = 7.5\text{--}8.8$; $B = 6.3\text{--}10.0$ (bothridial) and $L = 5.0\text{--}7.5$; $B = 6.3\text{--}7.5$ (antibothridial); $hsr = 6\text{--}7$. Strobila 56 mm long, maximum width 1250, about 280 acraspedote segments (Fig. 34). First segments behind velum short, enlarge in size, mature segments wider than long, from 500×840 to 700×1030 . In mature segments, genital atrium ventro-submarginal, in anterior third of segment; genital pores alternate irregularly. Cirrus sac elongated, $300\text{--}450 \times 80\text{--}110$ ($n = 5$), length:width ratio $3.8\text{--}4.1:1$, directed anteromedially, sac thin-walled; cirrus unarmed and coiled within sac. Ovary median, follicular, ovarian lobes $200\text{--}230$ (length) $\times 110\text{--}170$ (width), Mehlis' gland 80 in diameter, seminal receptacle 110×70 ; testes of variable shape, $60\text{--}80 \times 30\text{--}60$ ($n = 5$) in diameter, arranged in single layer; testes number $106\text{--}126$ ($n = 5$) per segment, encircle female genital complex and occupy entire medulla except for region of female genital complex and anterior to it; 7–9 testes anterior to cirrus sac. Vitelline follicles $20\text{--}40$ in diameter; egg diameter $20\text{--}25$; ventral osmoregulatory canals along margins of cortex, 6 in diameter.

Postlarva: $SL = 1650$, 1500 (Fig. 35); $SW = 790$, 770 ; $pbo = 820$, 820 ; $pv = 690$, 610 ; $pb = 480$, 430 ; $ppb = 110$, 80 ; $vel = 330$, 320 ; $BL = 460$ ($430\text{--}470$), 445 ($440\text{--}450$); $BW = 115$ ($110\text{--}120$), 120 ($118\text{--}122$); $BR = 4.0$, 3.7 ; $SP = 1.7:1.4:1$, $1.9:1.4:1$. Tentacles long, slender ($TL = 550\text{--}580$), $TSW = 40\text{--}45$; TW basal = $35\text{--}40$, TW metabasal and apical = $30\text{--}40$; basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths present. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous; characteristic basal armature absent. Hook shape varies from compact, rosethorn-shaped (bothridial) to smaller rosethorn-shaped hooks with elongated base (antibothridial); hooks increase in size towards metabasal part of tentacle on bothridial and antibothridial surface (Fig. 36). Hook size, metabasal, $L = 12.5\text{--}15.0$, $B = 11.8\text{--}13.3$ (bothridial) and $L = 11.3\text{--}12.5$; $B = 7.5\text{--}10.0$ (antibothridial); basal $L = 7.5\text{--}10.0$; $B = 8.8\text{--}11.3$

(bothridial) and $L = 5.0\text{--}7.5$; $B = 6.3\text{--}8.8$ (antibothridial); $hsr = 6\text{--}7$.

Remarks

Heteronybelinia estigmena (Dollfus, 1960) is a well-described tentaculariid. Palm (1995) reported this cestode as *Nybelinia alloiotica* Dollfus, 1960 from *Carcharhinus limbatus* in the Atlantic, the same host species as in the present study. Palm (1999) and Palm and Walter (2000) provided additional information on the species. *H. estigmena* resembles *H. perideraeus* (Shipley & Hornell, 1906) and *H. elongata* (Shah & Billequees, 1979) known from the coast of India. However, the hook size increases on both the bothridial and antibothridial tentacle surfaces in *H. estigmena*. In *H. elongata*, the hook size increases on the antibothridial tentacle surface only (Palm & Walter 1999), while in *H. perideraeus*, the basal and metabasal hook sizes are the same (Palm 1999). The present study represents the first record of the cestode from Australian waters. *Carcharhinus amblyrhynchoides* and *Sarda australis* represent new hosts for the species.

Heteronybelinia pseudorobusta sp. nov. (Figs 37–41)

Types

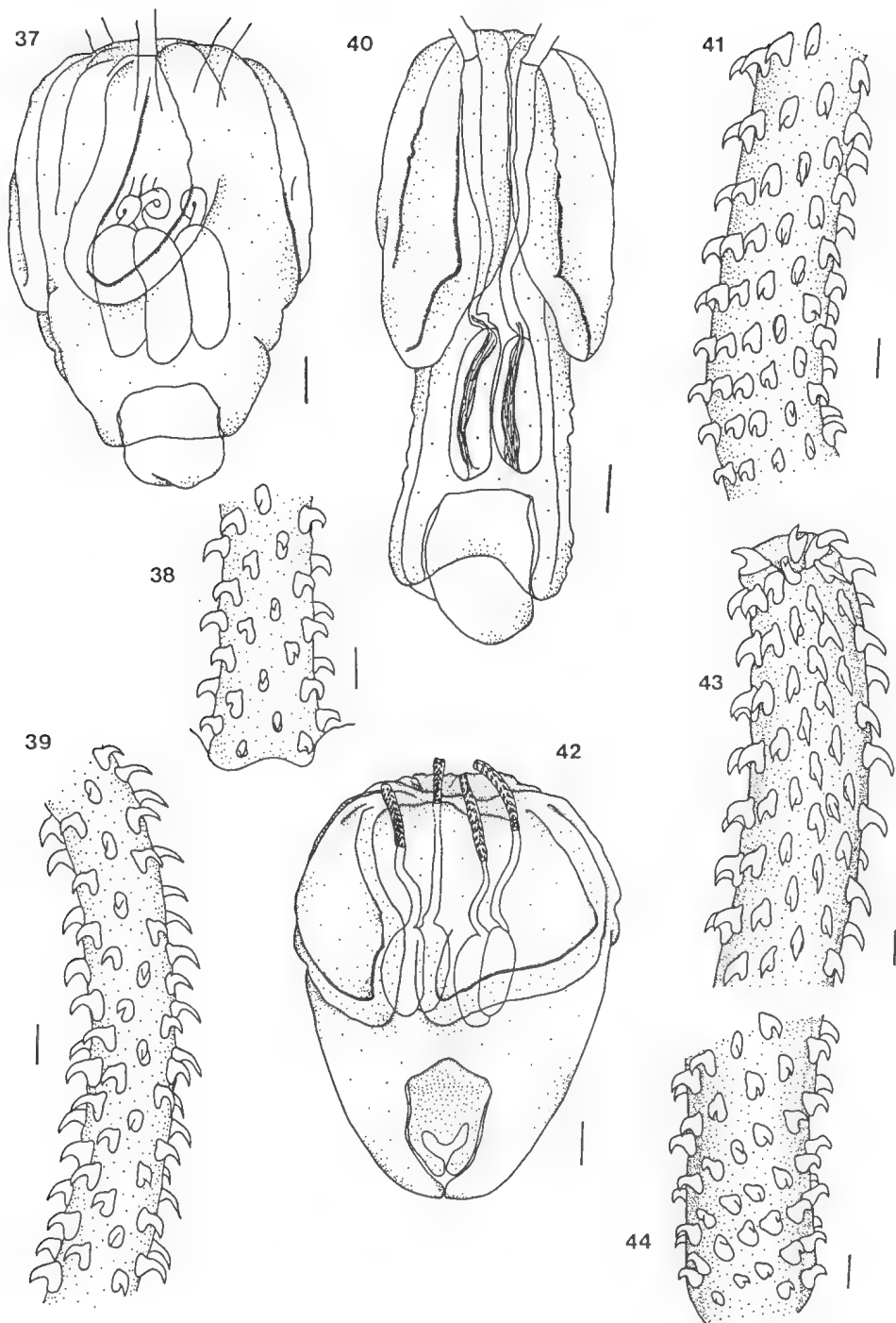
Holotype from gills of *Lepidotrigla modesta* Waite, 1899, Port Phillip Bay, Victoria, coll. R. Norman, 17.iii.1989 (SAM AHC 28341); 3 paratypes, same data (SAM AHC 28342).

Material examined

Types.

Description

Small form (holotype and one paratype): $SL = 960$ (Fig. 37), 730 ; $SW = 660$, 550 ; $pbo = 570$, 450 ; $pv = 420$, 270 ; $pb = 285$, 290 ; $app = 220$, 160 ; $vel = 70$, 60 ; $BL = 280$ ($275\text{--}285$), 298 ($275\text{--}315$); $BW = 150$ ($145\text{--}155$), 139 ($110\text{--}165$); $BR = 1.9:1$, $2.1:1$; $SP = 2.0:1.5:1$, $1.6:0.9:1$. Tentacle sheaths sinuous to spirally coiled; $TSW = 45.0\text{--}47.5$, $45.0\text{--}50.0$; TW basal $45.0\text{--}50.0$, metabasal $40.0\text{--}45.0$, basal tentacular swelling absent. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen, retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, characteristic basal armature absent (Fig. 38). Hook form changes from compact, rosethorn-shaped



FIGURES 37–41. *Heteronybelinia pseudorobusta* sp. nov. from *Lepidotrigla modesta*. 37. Scolex of small form SAM AHC 28314. 38. Basal armature. 39. Metabasal armature. 40. Scolex of large form SAM AHC 28342. 41. Metabasal armature. Scale bars: Figure 37, 100 µm; Figures 38–39, 20 µm; Figure 40, 100 µm; Figure 41, 15 µm. FIGURES 42–44. *Mixonybelinia cribbi* sp. nov. from *Platycephalus arenarius*. Holotype, QM G 218047. 42. Scolex. 43. Metabasal armature. 44. Basal armature. Scale bars: Figure 42, 200 µm; Figures 43–44, 20 µm.

(bothridial) to more slender hooks with stout base (antibothridial) (Fig. 39). Hook size in metabasal armature ranged between $L = 13.8\text{--}16.3$; $B = 11.3\text{--}13.8$ (bothridial) and $L = 16.3\text{--}17.5$; $B = 10.0\text{--}11.3$ (antibothridial), hooks of basal part of tentacle smaller, between $L = 10.0\text{--}11.0$; $B = 11.3\text{--}9.0$ (bothridial) and $L = 11.3\text{--}12.5$; $B = 8.8\text{--}10.0$ (antibothridial), continuously increasing towards the tip; $hsr = 6\text{--}7$.

Large form (2 paratypes): $SL = 1310$ (Fig. 40); 1310 ; $SW = 600$, 620 ; $pbo = 810$, 780 ; $pv = 580$, 500 ; $pb = 390$, 380 ; $app = 330$, 330 ; $vel = 280$, 310 ; $BL = 376$ ($360\text{--}390$), 321 ($310\text{--}330$); $BW = 124$ ($115\text{--}140$), 121 ($105\text{--}135$); $BR = 3.0:1$; $SP = 2.1:1.5:1$. Tentacle sheaths sinuous to spirally coiled; $TSW = 40\text{--}45$, $42.5\text{--}47.5$; TW basal $45.0\text{--}47.5$, metabasal $30.0\text{--}35.0$, $30.0\text{--}35.0$. Basal tentacular swelling absent, prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous, characteristic basal armature absent. Hooks change from compact and rosethorn-shaped (bothridial) to more slender hooks with a stout base (antibothridial) (Fig. 41). Hook size in metabasal armature between $L = 12.5\text{--}14.5$; $B = 11.3\text{--}12.5$ (bothridial) and $L = 14.5\text{--}15.5$; $B = 8.8\text{--}10.0$ (antibothridial), hooks of basal part of tentacle small, between $L = 8.8\text{--}10$; $B = 7.5\text{--}9.0$ (bothridial) and $L = 6.3\text{--}8.8$; $B = 6.3\text{--}7.5$ (antibothridial), increasing in size towards tip; $hsr = 6\text{--}7$.

Remarks

Heteronybelinia pseudorobusta sp. nov. is characterised by a heteromorphous tentacular armature consisting of small basal hooks increasing in size towards the metabasal region. The hook shape varies from rosethorn-shaped to slender hooks with a stout base on different surfaces of the tentacle. Small basal hooks which gradually increase in size towards the metabasal armature are characteristic of *Heteronybelinia robusta* (Linton, 1890). However, in contrast to *H. pseudorobusta* sp. nov., *H. robusta* has minute basal hooks, less than 5 in length, and the hook form is uniform along the tentacle. In the present specimens, the basal hook size is larger and the hook form is rosethorn-shaped. All other *Heteronybelinia* species differ in having a different hook shape or arrangement. Thus, the present specimens belong to a new species, *H. pseudorobusta* sp. nov., the name being derived from the similarity in hook arrangement to *H.*

robusta (Linton, 1890). *H. pseudorobusta* is a species without a characteristic basal armature and with basal hook sizes smaller than metabasal hook sizes. It therefore belongs to the *Heteronybelinia* species subgroup 'Aa' in Palm (1999).

Heteronybelinia pseudorobusta sp. nov. occurred in two different size groups, those smaller than 1 mm and those larger than 1.3 mm, respectively. Thus, the present description is an example of intraspecific morphological variability within species of *Heteronybelinia*, apparently due to scolex contraction during fixation.

Genus *Mixonybelinia* Palm, 1999

Mixonybelinia beveridgei (Palm, Walter, Schwerdtfeger & Reimer, 1997)

Material examined

From *Macruronus novaezelandiae* (Hector, 1871): 1 postlarva, west coast of Tasmania, coll. K. Sewell, June 1986 (QM G 218067).

Description

$SL = 3200$; $SW = 2750$; $pbo = 1750$; $pv = 850$; $pb = 1300$; $ppb = 80$; $vel = 950$; $app = 730$; $BL = 1226$ ($1150\text{--}1310$); $BW = 290$ ($240\text{--}320$); $BR = 4.2:1$; $SP = 1.3:0.7:1$. Tentacle sheaths sinuous to spirally coiled; $TSW = 100\text{--}130$. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal parts of bulbs. Basal tentacular swelling absent; TW basal = $110\text{--}120$, TW metabasal = $115\text{--}135$. Metabasal armature homeoacanthous, heteromorphous, characteristic homeomorphous basal armature consisting of about 6–7 rows of slender hooks with elongated shaft, stout base and strongly recurved at tip ($L = 31.3\text{--}40.0$, $B = 18.8\text{--}27.5$). Metabasal hooks strongly recurved, rosethorn-shaped with large base on antibothridial surface: $L = 50.0\text{--}52.5$, $B = 37.5\text{--}42.5$; slender falcate hooks with stout base on bothridial surface: $L = 55.0\text{--}60.0$, $B = 27.5\text{--}30.0$; $hsr = 6$.

Remarks

The present specimen is characterised by a homeomorphous basal armature of 6–7 rows of hooks and a heteromorphous metabasal armature of massive hooks, thus corresponding in form and size with specimens of *M. beveridgei* described from African waters by Palm et al. (1997). Other features are the large scolex size as well as TSW and TW . However, due to the contracted nature of

the scolex of the current specimen, values for scolex and bulb proportions as well as the tentacle sheaths differed, indicating the variability of these characters due to the degree of contraction of the scolex. The present finding represents a new host and locality record for *M. beveridgei*.

***Mixonybelinia cribbi* sp. nov.**

(Figs 42–44)

Types

Holotype, postlarva from *Platycephalus arenarius* Ramsay & Ogilby, 1886, Heron Island, Queensland, coll. J. Reddick, Jan. 1997 (QM G 218047).

Material examined

Types.

Description

Scolex craspedote, SL = 2920 (Fig. 42); SW = 2200; pbo = 1700; pv = 1020; pb = 730; ppb = 220; vel = 760; app = 780; BL = 615 (600–630); BW = 232 (220–240); BR = 2.7:1; SP = 2.3:1.4:1. Tentacle sheaths short; TSW = 50–65. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths not seen. Retractor muscles originate in basal part of bulbs. Basal tentacular swelling absent; TW basal = 70–75, TW metabasal = 65–75. Homeoacanthous, heteromorphous metabasal armature consisting of rosethorn-shaped hooks on bothridial and more slender hooks with stout base on antithridial surface (Fig. 43); characteristic homeomorphous basal armature (Fig. 44) consisting of about 4 rows of slender hooks with enlarged base and strongly recurved at tip (L = 12.5–17.5, B = 10.0–15.0 to 8.8–11.3). Metabasal hooks strongly recurved, rosethorn-shaped with large base on antithridial surface: L = 20.0–22.5, B = 18.8–21.3; slender falcate with stout base along bothridial surface: L = 21.3–23.7, B = 15.0–17.5; hsr = 6–7.

Remarks

M. cribbi sp. nov. resembles *M. beveridgei* in scolex size as well as in tentacular armature. Both species have a homeomorphous basal and a heteromorphous metabasal armature as well as a large scolex about 3 mm in length. However, *M. cribbi* sp. nov. is clearly distinguishable from *M. beveridgei* by having only 4 rows of basal hooks compared with 6 in *M. beveridgei*. In addition, the hooks have a distinctly enlarged base in *M. cribbi*

and all hooks are smaller (20–24 in *M. cribbi* compared with 46–68 in *M. beveridgei*, see Palm et al. 1997). The new species was named after Dr T. H. Cribb, Department of Parasitology, University of Queensland, Australia.

***Mixonybelinia edwinlintoni* (Dollfus, 1960)**

(Figs 45–53)

Material examined

From *Sphyrna lewini* (Griffith & Smith, 1843): 10 adults from stomach, Flat Top Island, Queensland, coll. B. G. Robertson, 23.x.1985 (SAM AHC 28324); 1 adult, Geraldton, Western Australia, coll. B. G. Robertson, 27.xi.1986 (SAM AHC 28323).

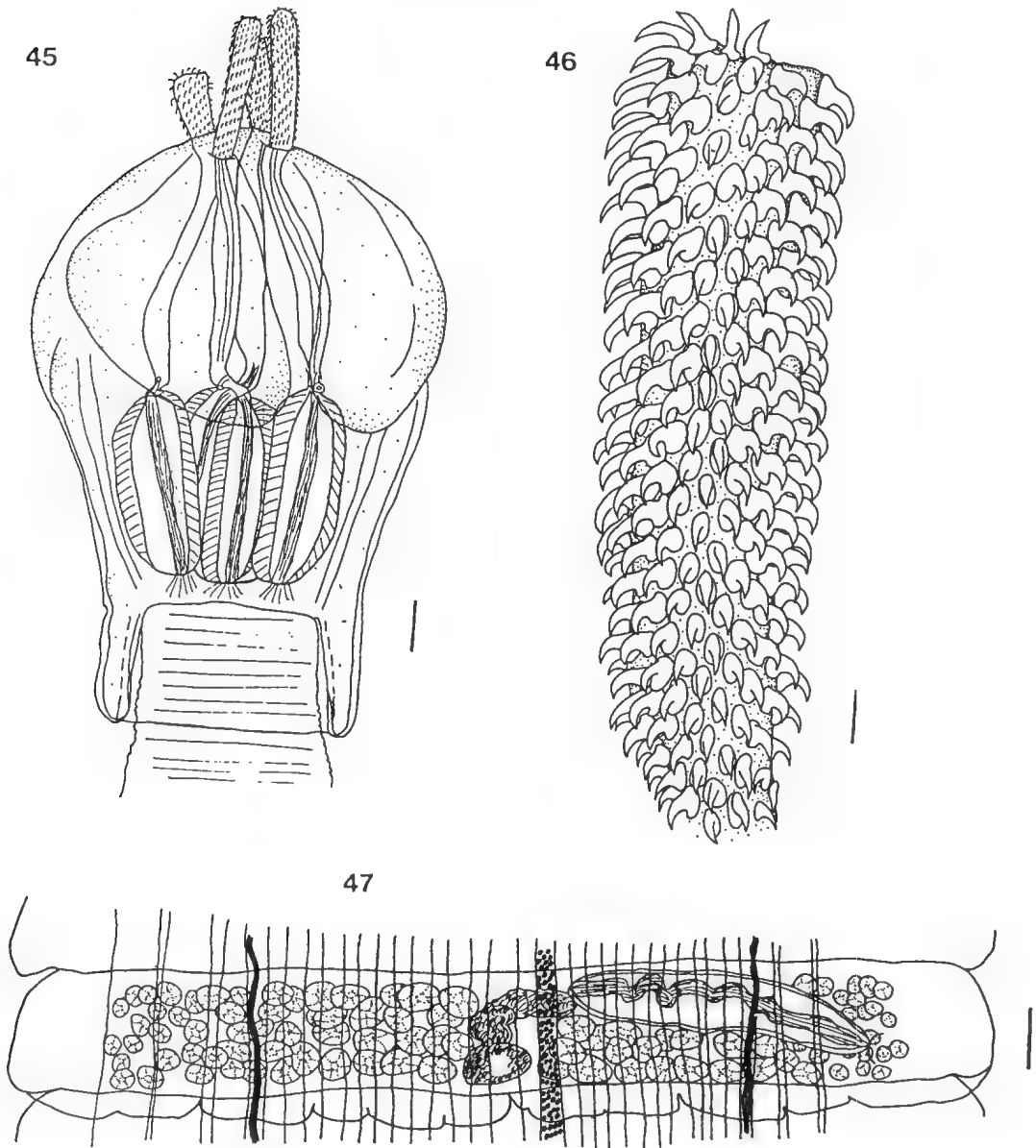
From *Rhynchobatus djiddensis* (Forsskal, 1775): 9 postlarvae from spiral valve, Moreton Bay, Queensland, coll. S. Butler, 17.iv.1980 (QM G 218048–218060).

From *Carcharhinus melanopterus* (Quoy & Gaimard, 1824): 1 postlarva, (QM G 4813).

Description

Adults: SL = 1780, 1620 (Fig. 45); SW = 1210, 1160; pbo = 1000, 1000; pv = 760, 690; pb = 620, 530; ppb = 60, 30; vel = 340, 330; BL = 585, 520, 520, 530, 490, within single specimen 580–600; BW = 235 (230–240); BR = 2.5:1; SP = 1.6:1.2:1. Tentacles robust; tentacle sheaths straight, TSW = 50–90. Prebulbar organs absent, muscular rings around basal part of tentacle sheaths visible in some specimens. Retractor muscles originate in basal part of bulbs: basal tentacular swelling absent; TW basal = 60–65; TW metabasal = 70–75. Metabasal armature homeoacanthous, heteromorphous (Fig. 46); characteristic homeomorphous basal armature consisting of about 10 rows of slender falciform hooks (Fig. 46). Metabasal hooks strongly recurved along antithridial surface: L = 20.0–25.0; B = 17.8–21.3; slender falcate hooks along bothridial surface: L = 32.5–35.0; B = 15.0–17.5. Basal hook size: L = 17.5–20.0, B = 10.0–13.8; hsr basal: 7–8; hsr metabasal: 8–9.

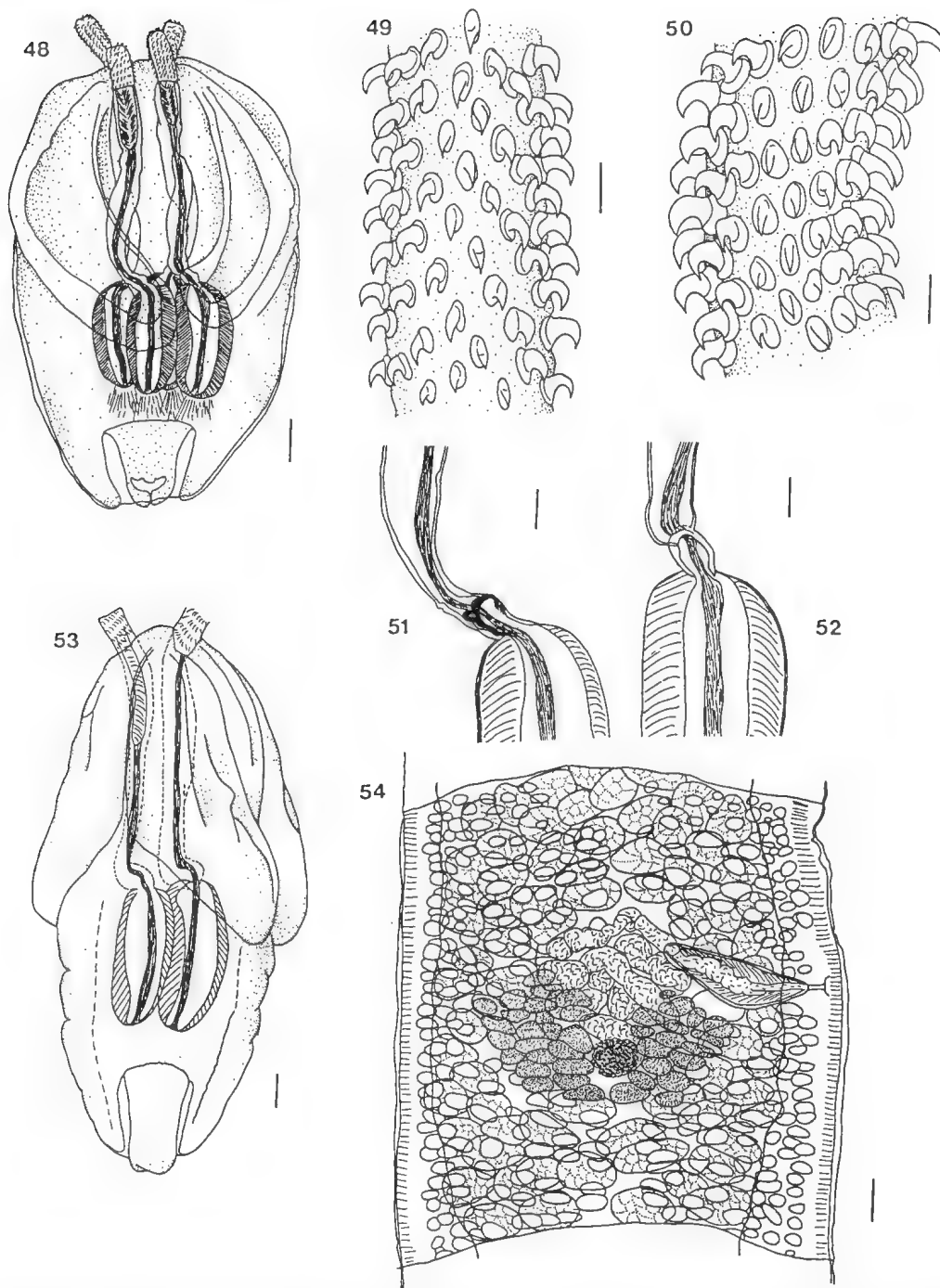
Largest cestode 53 mm, maximum width 880; 560 segments; strobila craspedote, velum irregularly scalloped, up to 50 wide; pre-mature (no ovary) segments (Fig. 47) wider than long, 100 x 1020 to 120 x 1020. Genital pores submarginal, in first third of segment; alternate irregularly. Cirrus sac elongate, 280–330 x 45–60 (n = 5) in mature segments, length:width ratio 5.7:1 (4.7–7.1:1), distal pole directed



FIGURES 45–47. *Mixonybelinia edwinlintoni* (Dollfus, 1960) from *Sphyrna lewini*. SAM AHC 28324. 45. Scolex. 46. Basal and metabasal armature. 47. Pre-mature proglottid. Scale bars: Figure 45, 150 μ m; Figure 46, 25 μ m; Figure 47, 60 μ m.

anteromedially, nearly reaching anterior end of segment; cirrus unarmed; internal and external seminal vesicles absent. Vas deferens coiled, extends to midline of segment, then posteriorly towards female genital complex. Testes in two groups, not confluent posterior to ovary, 80 (poral) and 116 (antiporal) (estimated), 30–40 in

size (central), smallest testes at margin of medulla, external to osmoregulatory canal (15–25), distributed in 2–3 layers, extend anterior to cirrus sac; seminal receptacle present. Small vitelline follicles encircle medulla, between 24 longitudinal muscle bands. Osmoregulatory canals 5 and 20 in diameter.



FIGURES 48–52. *Mixonybelinia edwinlintoni* (Dollfus, 1960) from *Rhynchobatus djiddensis*. QM G 218048–60. 48. Scolex. 49. Basal armature. 50. Metabasal armature, 20 rows from the base. 51–52. Bulb with tentacle sheath. Scale bars: Figure 48, 150 μ m; Figures 49–50, 25 μ m; Figures 51–52, 50 μ m. FIGURE 53. *M. edwinlintoni* from *Carcharhinus melanopterus*. QM G 4813. Scolex. Scale bar: 100 μ m. FIGURE 54. *Kotorella pronosoma* (Stossich, 1901) from *Dasyatis fluviorum*. QM G 218063. Mature proglottid. Scale bar: 50 μ m.

Postlarvae (from *R. djiddensis*): SL = 1600, 1500 (Fig. 48); SW = 1000, 1180; pbo = 1020, 950; pv = 680, 600; pb = 420, 470; ppb = 140, 120; vel = 280, 250; app = 280, 250; BL = 390 (370–410), 430 (410–440); BW = 188 (180–190), 163 (150–180); BR = 2.1:1, 2.6:1; SP = 2.4:1.6:1; 2.0:1.3:1. Tentacle sheaths straight, TSW = 40–85. Prebulbar organs absent, muscular rings and thickenings around basal part of tentacle sheaths visible in some specimens (Figs 51, 52). Retractor muscles originate in basal part of bulbs (Fig. 48); basal tentacular swelling absent; TW basal = 80, 80; TW metabasal = 70, 80. Homeomorphous basal armature of about 10 rows of slender falciform hooks (Fig. 49), metabasal armature homeoacanthous, heteromorphous (Fig. 50). Metabasal hooks strongly recurved along antiothridial surface: L = 22.5–25.0; B = 17.5–20.0; slender falcate hooks along bothridial surface: L = 23.8–26.3; B = 12.5–15.0. Basal hook size: L = 17.5–20.0, B = 12.5–13.8; hsr basal: 7–8; hsr metabasal: 8–9.

Postlarva (from *C. melanopterus*): SL = 1648 (Fig. 53); SW = 848; pbo = 912; pv = 768; pb = 432; ppb = 96; app = 320; vel = 240; BL = 429 (411–443); BW = 171 (158–177); BR = 2.5:1; SP = 2.1:1.8:1. Tentacles massive (TL = 630), TSW = 68–70; TW basal 77–80, TW metabasal 85–89, basal tentacular swelling absent. Prebulbar organs absent; muscular rings around basal part of tentacle sheaths not visible; retractor muscles originate at base of bulbs. Tentacular armature homeoacanthous, heteromorphous; characteristic basal armature absent. Hooks diminish in size towards base; hook shape varies from compact rosethorn-shaped (antiothridial) to slender rosethorn-shaped hooks with stout base (bothridial). Hook size, metabasal, rows 16–17, L = 23.7–25.2; B = 14.2–15.8 (antiothridial) and L = 25.2–26.8; B = 9.5–12.0 (bothridial); basal L = 17.4–19.0; B = 14.2–15.8 (antiothridial) and L = 17.4–19.0; B = 12.6–14.2 (bothridial); hsr = 7–8.

Remarks

Palm and Walter (2000) redescribed *Mixonybelinia edwinlintoni* (Dollfus, 1960) illustrating a distinctly different basal and metabasal armature within the species. While the metabasal armature has different hooks on the bothridial and antiothridial tentacle surface, the hooks of the basal armature appear to be homeomorphous. The arrangement of the hooks, together with their characteristic shape, and the scolex shape, indicate that the present specimens

belong to *M. edwinlintoni*. *Rhynchobatus djiddensis* and *Carcharhinus melanopterus* represent two new hosts for the species.

Prior to the re-description of *M. edwinlintoni*, Palm (1999) erected *Heteronybelinia heteromorphi*, a species which is also very similar to the present material. In *H. heteromorphi* the basal armature is heteromorphous, while in *M. edwinlintoni* it is homeomorphous. In addition, the type material of *H. heteromorphi* was described as being acraspedote while *M. edwinlintoni* is craspedote (Fig. 47). Interestingly, both species occur within the same host genus, *Sphyrna*. Other characters such as the massive scolex form, the heteromorphous metabasal armature, and the testis sizes are similar in both species. The type material of *H. heteromorphi* needs to be re-examined to confirm the differences between the species.

Mixonybelinia southwelli (Palm & Walter, 1999)

Material examined

From *Makaira indica* (Cuvier, 1832): 1 postlarva, Cape Bowling Green, Queensland, coll. P. Speare, 18.ix.1987 (QM G 218061).

From *Chaerodon venustus* (DeVis, 1885): 1 postlarva, Heron Island, Queensland, coll. R. Bray, 30.i.1991 (QM G 218062).

Description

SL = 2000, 1550; SW = 1050, 690; pbo = 1030, 890; pv = 850, 660; pb = 440, 590; ppb = 40; vel = 450, 220; app = 670, 270; BL = 411 (400–425), 548 (520–580); BW = 153 (140–165), 153 (140–170); BR = 2.7:1, 3.6:1; SP = 2.3:1.9:1, 1.5:1.1:1. Tentacle sheaths spirally coiled; TSW = 55–60, 50–60. Prebulbar organs absent, muscular rings around the basal part of tentacle sheaths not seen; retractor muscles originate in basal part of bulbs; tentacular swelling absent; TW basal = 50.0–55.0, 47.5–55.0, TW metabasal = 35–47, 30–35.

Armature homeoacanthous, heteromorphous; characteristic basal armature consisting of about 14–16 rows. Antiothridial metabasal hooks massive, rosethorn-shaped, L = 15.0–17.5, 15.0–16.3, B = 13.7–15.0, 15.0–17.5; bothridial hooks more slender and slightly curved with stout base, L = 18.7–20.0, 17.5–20.0, B = 11.3–12.5, 11.3–13.8. Basal armature homeomorphous, hooks falciform with stout base and strongly recurved tip, L = 15.0–22.5,

18.8–21.3; B = 7.5–8.7, 7.0–8.0; hsr basal = 6–7, hsr metabasal = 5–6.

Remarks

The postlarva from *Chaerodon venustus*, collected at Heron Island, is similar in scolex size and proportions, armature pattern and hook sizes to those described for *M. southwelli* by Palm and Walter (1999). Differences in scolex measurements of the specimen from *Makaira indica* are probably due to the shrunken condition of that specimen. The change in armature pattern from falciform basal hooks to heteromorphous rosethorn-shaped metabasal hooks is characteristic for *M. southwelli*. The distribution of the species is extended to eastern Australian waters, and *Makaira indica* and *Chaerodon venustus* represent new hosts for the species.

Genus *Kotorella* Euzet & Radujkovic, 1989

Kotorella pronosoma (Stossich, 1901) (Fig. 54)

Material examined

From *Dasyatis fluviorum* Ogilby, 1908: 2 adults, Moreton Bay, Queensland, coll. S. Butler, 26.ix.1980 (QM G 218063–218064).

Description

SL = 570, 660; SW = 200, 200; pbo = 400, 390; pv = 385, 510; pb = 80, 85; vel = 110, 80; BL = 71 (70–73), 78 (71–88); BW = 39.4 (37.5–40.0), 40.0 (35.3–45.0); BR = 1.8:1, 2.0:1; SP = 5.0:4.8:1, 4.6:6.0:1. TW basal = 17.5, 22.5. Basal tentacular swelling absent. Tentacle sheaths straight; TSW = 11.3–15.0, 5.5–15.0. Prebulbar organs and muscular rings around basal part of tentacle sheaths absent; retractor muscles originate in basal part of bulbs. Tentacular armature homeoacanthous, heteromorphous; basal hooks on bothridial surface L = 6.3–7.5, 6.3–7.5, B = 5.0–6.0, 5.0–6.0, smallest hooks on antibothridial surface L = 2, increasing in size towards metabasal region. Small, incomplete worms to 15 mm long, maximum width 570; 90 segments. Strobila acraspedote; pre-mature segments 30 x 110 – 260 x 360, mature segments longer than wide or wider than long, 480 x 430 to 550 x 620 (Fig. 54). In second specimen, mature segments 500 x 440 to 550 x 650, and pre-gravid (with some eggs) segments 320 x 710 to 750 x 620. Genital pores submarginal, 210 from anterior margin; alternate irregularly. Cirrus sac elongate,

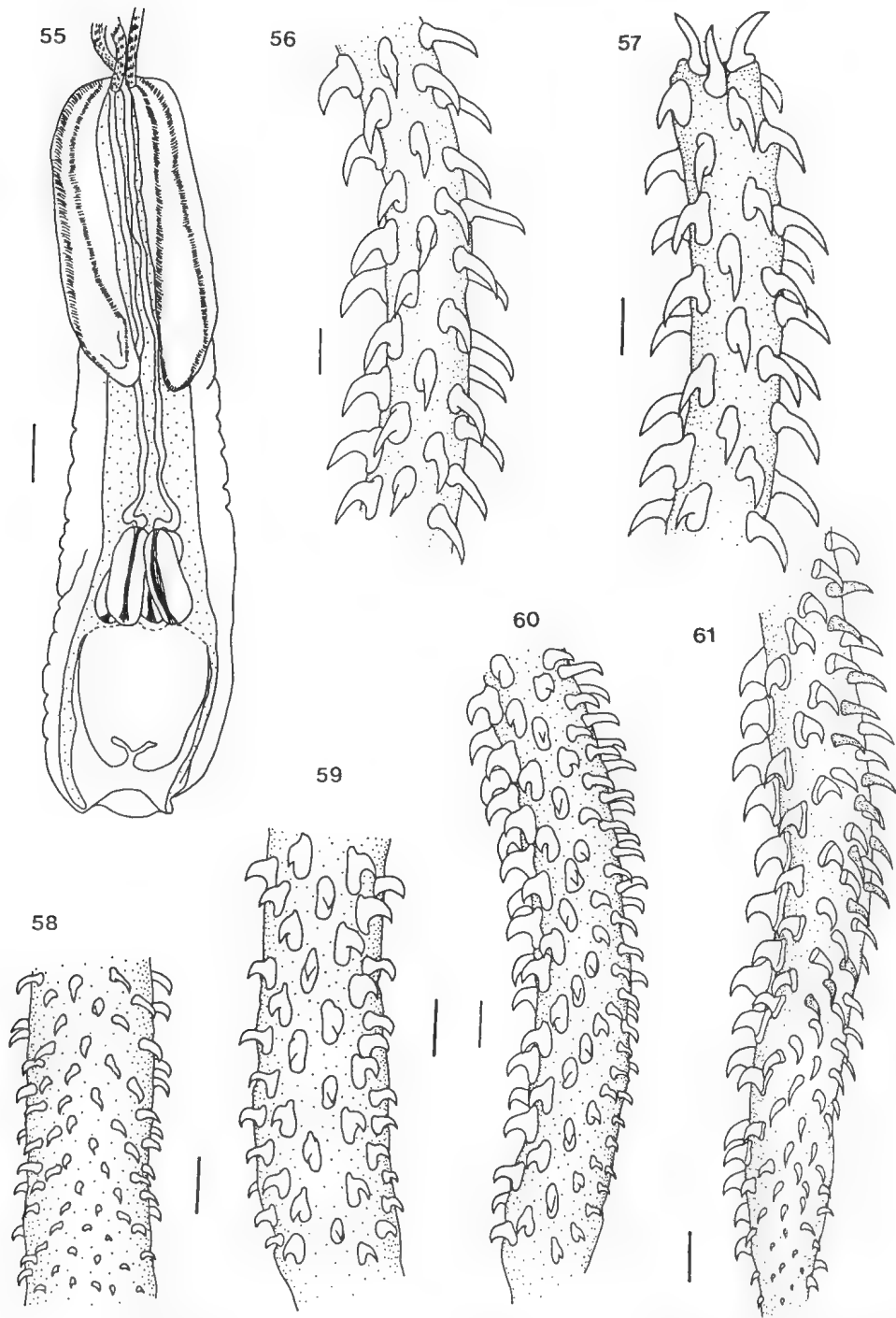
150–250 x 30–60 (n = 5) in mature segments, length:width ratio 4.4:1 (4.0–5.0:1); cirrus unarmed; internal and external seminal vesicles absent. Vas deferens in large coils, extends to midline of segment, then posteriorly towards female genital complex. Testes 86 (81–100) in number, 45–85 in size (central), smallest testes 20–50 (peripheral), distributed in single layer, confluent posterior and anterior to ovary. Ovary median, ovarian lobes 110–200 x 100–150; Mehlis' gland small, situated between ovarian lobes. No vitelline follicles in centre of the segment, follicles 33 (25–45) in diameter. No uterus observed, spherical eggs appear in parenchyma, egg diameter 22 (15–40).

Remarks

The morphology of *Kotorella pronosoma* (Stossich, 1901) is summarised by Euzet and Radujkovic (1989), Palm and Walter (1999) and Palm and Overstreet (2000). The present specimens from Moreton Bay correspond in scolex size and proportions as well as in the tentacular armature with the other described specimens. The sole difference noted was in testis number which exceeded 80 per segment in the specimens described. The species has previously been found in rays such as *Aetobatus narinari* (Euphrasen, 1790) (see Palm & Overstreet 2000), *Himantura imbricata* (Bloch & Schneider, 1801), *Rhynchobatus djiddensis* (see Shipley & Hornell 1906; Palm & Walter 1999) and *Dasyatis pastinaca* (Linnaeus, 1758) (see Euzet & Radujkovic 1989; Palm & Walter 2000). *Dasyatis fluviorum* represents a new host record, and the range of distribution is extended to eastern Australian waters. The present finding suggests a cosmopolitan distribution for the species. Previously, the nearest known occurrence of this cestode to Australia was from the Java Sea under the name *Nybelinia narinari* (MacCallum, 1917), now a synonym of *Kotorella pronosoma* (see Palm & Overstreet 2000).

Kotorelliella gen. nov.

Diagnosis: Tentacles elongate, slender; retractor muscle originates at base of bulbs. Metabasalar tentacular armature homeoacanthous, heteromorphous; hooks on bothridial surface uncinuate becoming slender towards antibothridial surface. Basal hooks heteromorphous; characteristic basal armature present, arranged in a heteroacanthous atypica pattern with



FIGURES 55–61. *Kotorelliella jonesi* gen. et sp. nov. from *Taeniura lymnaea*. Holotype, QM G 218065. 55. Scolex. 56–57. Metabasal and apical armature, external view. 58. Basal armature, bothridial view. 59. Basal armature, antiothridial view. 60–61. Basal towards metabasal armature, external view. Note the interpolated hooks as in Fig. 61. Scale bars: Figure 55, 150 μ m; Figures 56–61, 10 μ m.

interspersed hooks on the antiothridial tentacle surface. Hooks solid. Strobila unknown.

Type-species: *Ko. jonesi* sp. nov.

***Kotorelliella jonesi* sp. nov.**

(Figs 55–61)

Types

Holotype, 1 postlarva from the spiral valve of *Taeniura lymma* (Forsskål, 1775), Heron Island, Queensland, coll. I. Beveridge & M. K. Jones, 11.vii.1998 (QM G 218065).

Material examined

Holotype.

Description

Scolex compact, 4 elongated bothridia, with hook-like microtriches along bothridial borders. Posterior margins of bothridia free, not fused with peduncle. SL = 1910 (Fig. 55); SW = 390; pbo = 800; pv = 1140; pb = 260; vel = 460; BL = 259 (250–265); BW = 82.5 (80–85); BR = 3.1:1; SP = 3.1:4.4:1. Tentacles long and slender; TW basal and metabasal = 21.2–23.8; TW apical = 17.5–20; basal tentacular swelling absent. Tentacle sheaths straight; TSW = 15.0–17.7. Prebulbar organs and muscular rings around basal part of tentacle sheaths absent; retractor muscles originate in basal part of bulbs. Metabasal (Fig. 56) and apical (Fig. 57) armature homeoacanthous, heteromorphous. Rosethorn-shaped hooks with anterior extension of base cover bothridial tentacle surface (L = 13.5–15.0, B = 7.5–10.0); antiothridial surface with slender spiniform hooks, recurved at tip (L = 15.0–17.5, B = 5.0–6.3); hooks decrease in size towards apical armature; hook shape remains constant (bothridial: L = 11.3–13.7, B = 10.0–11.2; antiothridial: L = 12.5–13.7, B = 4.5–5.5). Basal armature (Figs 58–61) with additional hooks interspersed on antiothridial surface; hook pattern heteroacanthous atypica, consisting of about 5 rows of hooks on bothridial (Fig. 59) and 9–10 rows on antiothridial (Fig. 58) tentacle surface; basal hooks on bothridial surface L = 6.3–10.0, B = 6.3–8.8, on antiothridial surface L = 2.0–10.0, B = 1.5–3.8, continuously increasing in size from base of tentacle towards metabasal armature (Figs 60–61).

Remarks

The holotype of *Kotorelliella jonesi* gen. et sp. nov. has a unique form of armature within the

Tentaculariidae, changing from a homeoacanthous, heteromorphous hook pattern with rosethorn-shaped hooks in the metabasal armature to a heteroacanthous atypica hook pattern in the basal armature. The size of hooks in the basal and apical regions is smaller than in the metabasal region.

On the basis of the scolex morphology, *Ko. jonesi* sp. nov. appears to be similar to *Kotorella pronosoma*. Both species have an elongated scolex, four elongated and slender bothridia with free margins, and short oval bulbs. In both species, the metabasal armature is heteromorphous, with hooks changing from uncinat on the bothridial surface to elongate on the antiothridial surface. Both species have a band of hook-like microtriches along bothridial borders, which are clearly visible using light microscopy. Such a microtrich pattern is characteristic for tentaculariid trypanorhynch cestodes.

The basal armature of *K. pronosoma* is homeoacanthous, but that of *Ko. jonesi* sp. nov. is unusual, having additional hooks interspersed between the oblique spirals of hooks. Thus, the basal tentacular armature is heteroacanthous atypica. The basal region is homeoacanthous in *Nybelinia*, *Heteronybelinia* and *Mixonybelinia*, but in *Tentacularia*, the bothridial surfaces of the tentacle have extra rows of small hooks (see Beveridge & Campbell 1996). The unique feature of the tentacular armature suggests that the erection of a new genus is justified, even though it is known only from the larval stage.

The new species was named after one of the collectors, Dr M. K. Jones, from the Centre for Microscopy and Microanalysis, University of Queensland, Australia.

Unidentified material

The following additional material, some of which represent new host records, was examined but could not be assigned to a species:

Nybelinia sp. from the spiral valve of *Rhynchobatus djiddensis*, Flat Top Island, Queensland, coll. B. G. Robertson, 25.x.1985 (SAM AHC 28325)

Nybelinia sp. from the spiral valve of *Notorhynchus cepedianus* (Péron, 1807), south coast Kangaroo Island, South Australia, coll. B. G. Robertson, 10.ii.1985 (SAM AHC 28327)

Nybelinia sp. from the stomach of *Notorhynchus cepedianus*, Young Rocks, Kangaroo Island, South Australia, coll. B. G.

Robertson, 23.v.1985 (SAM AHC 21354, 28328)

Heteronybelinia sp. from the spiral valve of *Carcharhinus amblyrhynchoide*s, Tommy Cut Mouth, Northern Territory, coll. B. G. Robertson, 19.ix.1986 (SAM AHC 18326).

DISCUSSION

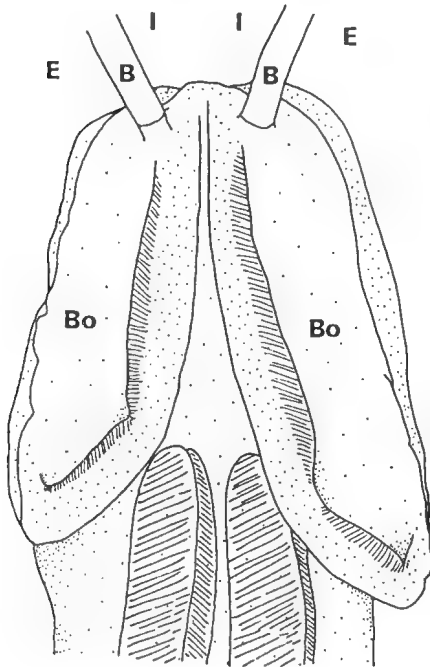
The present study provides an overview for the first time of the tentaculariid trypanorhynch fauna from the Australian region. Three new species are added to the genus *Nybelinia*, two to *Heteronybelinia* and one to *Mixonybelinia*, with the latter two genera, as well as *Kotorella*, reported from the Australian region for the first time. In addition, a new genus *Kotorelliella* gen. nov., is erected, which is characterised by a homeoacanthous, heteromorphous metabasal armature and a heteroacanthous basal armature. Other features such as the elongated, widely

spaced bothridia and the short bulbs appear similar to *Kotorella*.

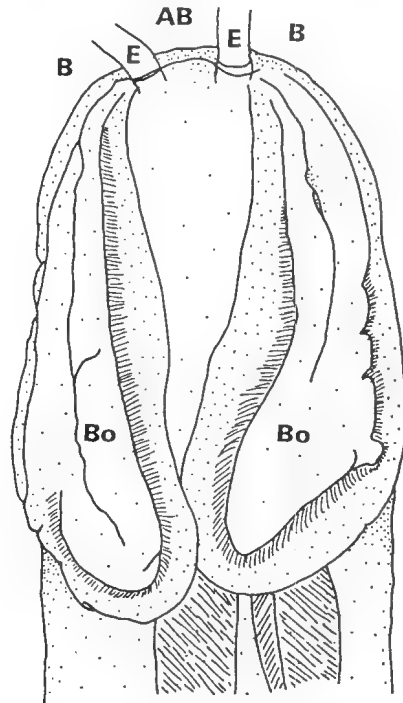
The tentaculariid trypanorhynch fauna in Australian waters is relatively species rich with 22 (48 %) of the total of 46 known species occurring in these waters. Several of the new species may be endemic. However, the distribution of many species is still imperfectly known and a number of species previously thought to be endemic to a specific region have subsequently proven to be cosmopolitan (Palm et al. 1997; Palm 1999; Palm & Walter 1999, 2000). Reasons for broad distributions within tentaculariid trypanorhynchs may relate to life-cycle patterns, including widely distributed fish intermediate and elasmobranch definitive hosts. Another reason might be the low host specificity of the parasites, particularly in the intermediate host (Palm et al. 1997; Palm & Walter 2000).

It is difficult to clearly distinguish between

62.



63



FIGURES 62–63. Schematic drawing of scolex of *Heteronybelinia pseudorobusta* sp. nov. from *Lepidotrigla modesta*, illustrating the arrangement of the different tentacle surfaces within tentaculariid trypanorhynchs. 62. View from bothridial surface, with bothridial borders merging at the apex of the scolex. 63. View from external surface, with bothridial borders widely spaced. Abbreviations, AB = antibothridial view, B = bothridial view, Bo = bothridia, E = external view, I = internal view.

some tentaculariid species solely on the basis of the tentacular armature (eg *N. strongyla*), and additional taxonomic characters are required. To date, the strobilae of only a few tentaculariid species have been described in detail. The present study demonstrates that, apart from the number and size of different genital structures, the cirrus sac length:width ratio might be a useful character as, for example, in *H. australis* sp. nov. and *N. hemipristis* sp. nov. The position of the anterior end of the cirrus sac and the distance of the genital pore from the anterior end of the segment, as well as the number of layers of testis, whether the testes are confluent posterior to the ovary, and the number of testes anterior to the cirrus sac appear to be useful taxonomic features. Further species descriptions are needed to show whether or not these characters are variable, as is observed in a number of scolex characters, or whether they can be used more widely in tentaculariid systematics.

During this and previous studies, it became evident that the descriptions of the different tentacular surfaces of trypanorhynch cestodes used by Dollfus (1942) and Campbell and Beveridge (1994) may be difficult to apply to larval tentaculariids. In many cases it was hard to identify the various tentacle surfaces. For a better understanding of the position of the four tentacles within tentaculariid trypanorhynchs, the following two schematic illustrations are given (Figs 62, 63) as they may help to standardise the orientation of the different tentacle surfaces within tentaculariid trypanorhynchs. The determination of tentacle orientation is based upon whether the bothridial borders merge at the apex of the scolex (Fig. 62) or whether they are widely spaced (Fig. 63). The former figure shows the bothridial and the latter the external view of the tentacle surfaces.

The description of *Kotorelliella jonesi* gen. et sp. nov. is of particular interest since its armature comprises both homeomorphous and heteromorphous components (Campbell & Beveridge 1994; Palm 1995, 1997). The species seems to be closely related to *Kotorella pronosoma*, which has a similar scolex morphology and metabasal armature. Both species have characteristic microtriches along the bothridial borders, which appear similar to those of *Tentacularia coryphaenae* and species of *Nybelinia* (see Palm & Overstreet 2000). Although Beveridge et al. (1999) could not align

Kotorella with the other tentaculariid genera using cladistic analyses, we consider that *Kotorella pronosoma* and *Kotorelliella jonesi* belong to the Tentaculariidae since they possess a homeoacanthous metabasal armature and, more importantly, bands of hook-like microtriches along the bothridial borders. The latter character has as yet only been described for tentaculariid trypanorhynchs.

Following the classification of Dollfus (1942), only the metabasal armature is considered in classifying the tentacular armature. However, in more recent classifications, trypanorhynchs with a distinct basal armature such as *Mixodigma leptaleum* Dailey & Vogelbein, 1974, *Paroncomegas araya* (Woodland, 1934) and *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) have been placed in distinctive genera based in part on the basal armature (Campbell & Beveridge 1994; Campbell et al. 1999; Palm 1999). *Kotorelliella jonesi* has thus been placed in a new genus. Interestingly, *K. jonesi* represents a transition from homeoacanthous towards heteroacanthous armature as suggested by Campbell and Beveridge (1994, p. 57, lines 7–11).

In summary, tentaculariid trypanorhynchs show considerable morphological variability, as can be seen by differences in scolex morphology between the genera *Nybelinia*, *Heteronybelinia* and *Mixonybelinia*, and between *Kotorella* and *Kotorelliella*. The tentacular armature also differs between the species, varying from homeoacanthous and homeomorphous (*Nybelinia*, *Mixonybelinia*) to homeoacanthous and heteromorphous (*Heteronybelinia*, *Kotorella*, *Mixonybelinia*) patterns. *Kotorelliella* has a homeoacanthous metabasal and a heteroacanthous basal hook pattern. Additional methods, such as molecular genetic studies, might help to resolve not only species relationships but also the phylogenetic relationships of the species and species groups within this large trypanorhynch family.

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TWO NEW SPECIES OF THE GENUS LEPANUS BALTHASAR FROM SOUTH AUSTRALIA (COLEOPTERA : SCARABAEIDAE)

E. G. MATTHEWS & T. A. WEIR

Summary

Ball-rolling dung beetles of the tribe Scarabaeini are recorded for the first time from South Australia. The new species *Lepanus penelopae* and *L. loftyensis* are described from southern Eyre Peninsula and the Mount Lofty Block respectively, and are compared with other species of the genus. There are brief remarks comparing *Lepanus Balthasar* with the related genera *Sauvagesinella* Paulian and *Aptenocanthus* Matthews.

TWO NEW SPECIES OF THE GENUS *LEPANUS* BALTHASAR FROM SOUTH AUSTRALIA (COLEOPTERA: SCARABAEIDAE)

E. G. MATTHEWS & T. A. WEIR

MATTHEWS, E. G. & WEIR, T. A. 2002. Two new species of the genus *Lepanus* Balthasar from South Australia (Coleoptera: Scarabaeidae). *Records of the South Australian Museum*. 35(1): 79–84.

Ball-rolling dung beetles of the tribe Scarabaeini are recorded for the first time from South Australia. The new species *Lepanus penelopae* and *L. loftyensis* are described from southern Eyre Peninsula and the Mount Lofty Block respectively, and are compared with other species of the genus. There are brief remarks comparing *Lepanus* Balthasar with the related genera *Sauvagesinella* Paulian and *Aptenocanthus* Matthews.

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At the time of the revision by Matthews (1974) of the Australian Scarabaeini, generally known as ball-rolling dung beetles, it was believed that this group was absent from South Australia, although it was known from Victoria and Western Australia. However, in 1979 P. Greenslade obtained specimens of an undescribed species of the genus *Lepanus* Balthasar, which belongs to this tribe, in the Marble Range of southern Eyre Peninsula; and in 1982 another undescribed species of the same genus was collected during extensive pitfall trapping undertaken by J. and P. Greenslade in Kuitpo Kyeema Forest, southern Mount Lofty Ranges, in connection with a project to determine the effects of fire on the forest-floor fauna. Then in 1999 and 2000, more specimens of the second species were picked up by members of the Biological Survey of South Australia in the area of Mount Remarkable at the extreme northern end of the Mount Lofty Block environmental province, as well as near the Barossa Valley, using unbaited pitfall traps. Altogether, the two species are now known from five collection localities (Fig. 1), all situated on low mountain ranges at altitudes from 300 to just over 500 m. Kangaroo Island is part of the Mount Lofty Block but pitfall traps baited with human faeces, set throughout the island by one of the authors (EGM) in November 1990, failed to collect any *Lepanus*.

Lepanus is known from New Guinea, where it was first described, and from densely vegetated mesic and humid habitats along the northern, eastern and southern coasts of Australia as far west as the tingle forest near Walpole, Western

Australia (Matthews 1974). The habitat is leaf litter, and food, where known, consists of vertebrate faecal matter. The descriptions below bring the total number of described Australian species of *Lepanus* to 23, but several undescribed species have been collected in recent years in eastern montane forests (R. Storey, pers. comm.).

Specimens are deposited in the South Australian Museum, Adelaide (SAMA); the Australian National Insect Collection, Canberra (ANIC); the Queensland Museum (QMBA); and the Queensland Department of Primary Industries collection at Mareeba (DPIM).

All figures except the map are by the senior author.

DESCRIPTIONS OF NEW SPECIES

Lepanus penelopae sp. nov.

(Figs 1, 2, 3, 5, 7, 9, 12)

Holotype

'S. Aust. Eyre Pen. Marble Rge. Dense broombush. Pitfall. 4.10.79. P.J.M. Greenslade', male, SAMA.

Paratypes

Same data as holotype, 1 male and 5 females, ANIC, SAMA.

Description

Body uniformly piceous and nitid, legs rufous. Total length 5.0–6.0 mm. Maximum width across

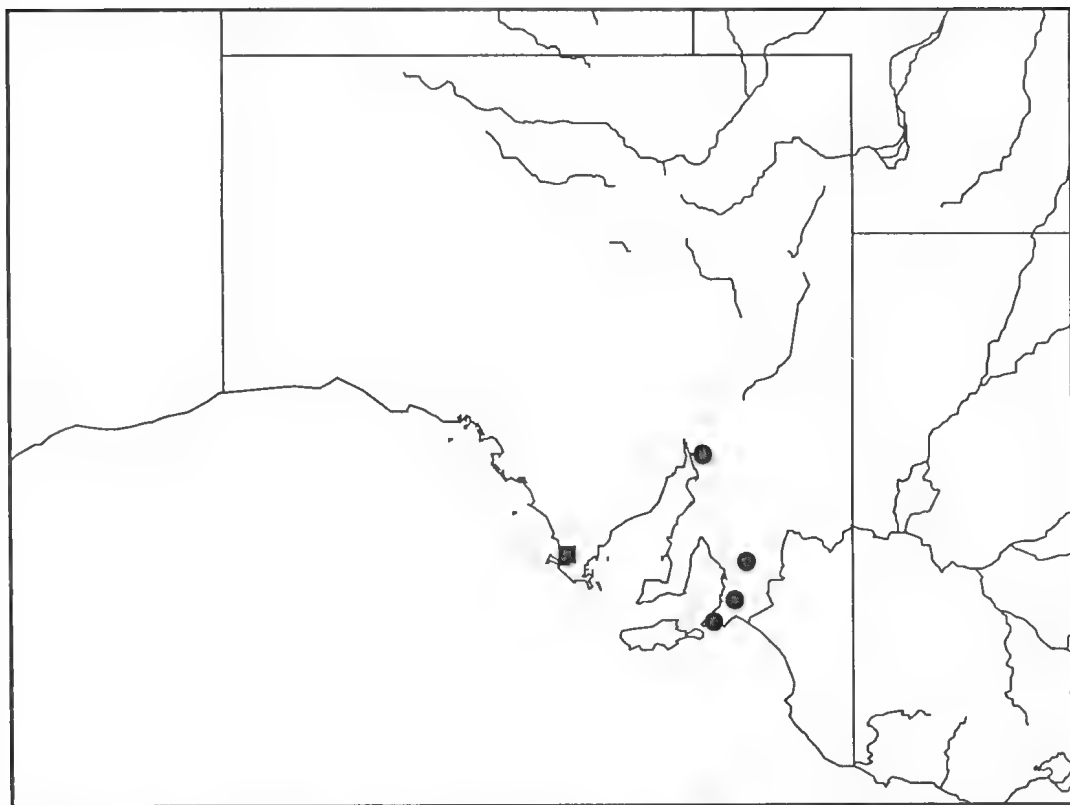


FIGURE 1. Known distribution in South Australia of species of *Lepanus*. ■, *L. penelopae*; ●, *L. loftyensis*.

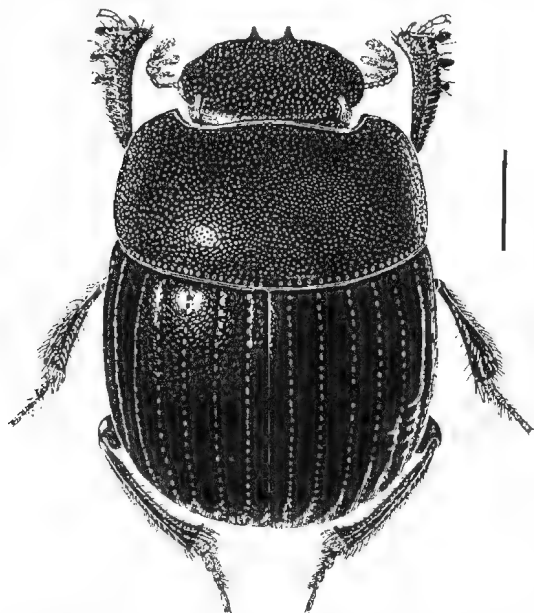
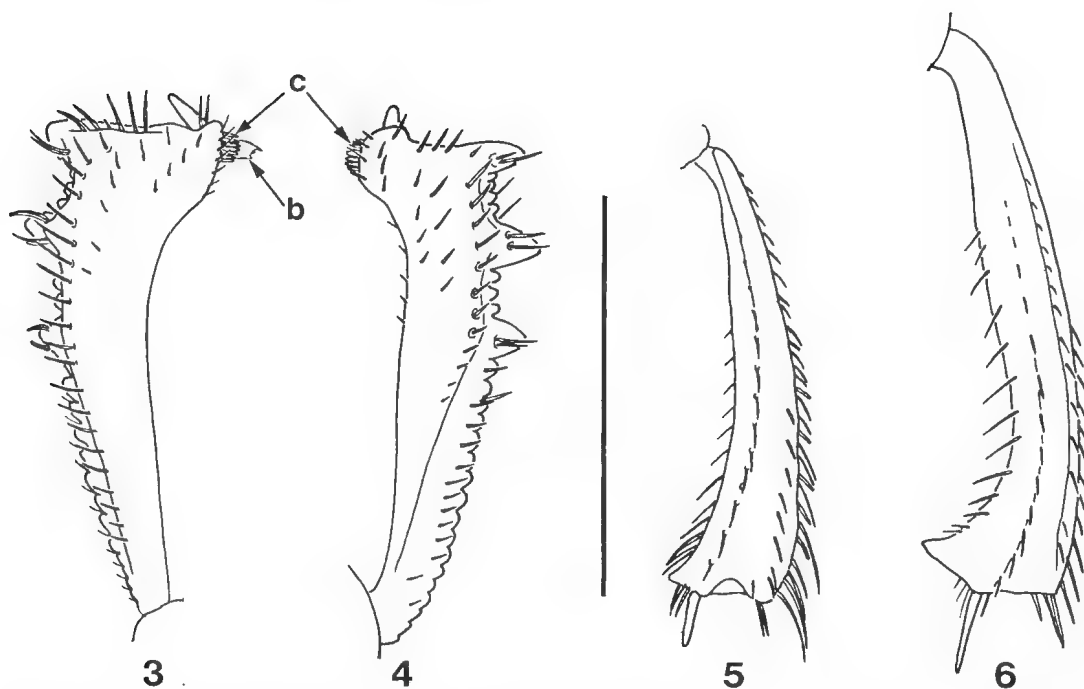


FIGURE 2. *Lepanus penelopae* male, habitus. Scale line 1 mm.

elytra 3.4–3.6 mm. *Head* – Dorsal surface even, very densely punctate with small shallow punctures not running together, some bearing short, very fine recumbent setae. Dorsal part of eye small, its maximum width contained about 25 times in interocular distance. *Prothorax* – Anterior angles subquadrate. Sides of pronotum rounded, widest at broadly rounded posterior angles. Dorsal surface very densely and uniformly finely punctate, punctures separated by distances equal to a little more than their diameter, glabrous. *Elytra* – Striae shallowly impressed with regularly spaced moderately deep punctures separated by 2–4 diameters. Intervals nearly flat, smooth with very slightly uneven surface, glabrous, with minute punctures. *Hind wings* – Absent. *Sterna* – Meso- and metasterna impunctate medially with large shallow cicatricose punctures laterally, glabrous. *Legs* – Protibia with three large teeth on outer edge, which is serrate between teeth and proximal to them. Claws (Fig. 7) a little expanded basally but not distinctly angulate or dentate. *Abdomen* – Pygidium (Fig. 9) with a very deep



FIGURES 3-6. Tibiae of males in dorsal view. 3, *L. penelopae*, left protibia; 4, *L. loftyensis*, right protibia; 5, *L. penelopae*, right metatibia; 6, *L. loftyensis*, right metatibia. b, brush of stiff setae; c, comb of flattened bristles. Scale line 1 mm.

basal groove across whole width of disc, groove narrower and shallower in middle, surface inside it transversely striated. Disc very finely punctate, glabrous. Aedeagus as in Fig. 12. *Sexual dimorphism* – Male with rounded expansion of inner apical end of protibia bearing apical comb of short wide flattened bristles (Fig. 3, c) and on lower surface a brush of long setae which is directed outwardly parallel to surface, extending beyond edge of comb (Fig. 3, b). Metatibia of male (Fig. 5) a little expanded at inner apical edge and bearing small apical tooth there.

Remarks

In the key to the species of *Lepanus* published by Matthews (1974), *L. penelopae* will go to couplet 16 because it has three protibial teeth, and then to couplet 18 because it has a transverse groove on the pygidium and glabrous dorsal surfaces. However, it does not have dentate claws as also required by this couplet. It can then be forced through couplets 19 and 20 to end up with *L. illawarrensis* Matthews of New South Wales, which appears to be the most closely related species, sharing many aspects of structure and secondary sexual characters. *L. penelopae* differs

from *L. illawarrensis* in having simple claws, non-geminate elytral striae with much deeper strial punctures, the pygidial groove more strongly narrowed in the middle, the basal ridge of the pygidium straight in the middle, no trace of a median tubercle on the metasternum of the male, male hind tibia not twisted, and somewhat differently shaped aedeagal parameres.

Etymology

This species is named after Penelope Greenslade, who collected it as well as many of the other specimens of *Lepanus* described in this paper.

Lepanus loftyensis sp. nov.

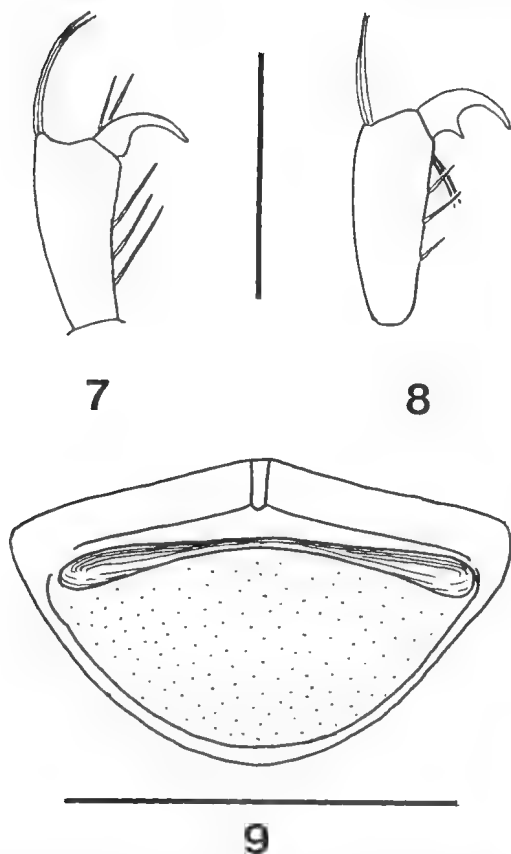
(Figs 1, 4, 6, 8, 10, 11)

Holotype

'S. AUST. Pitfalls Kuitpo Kyeema Forest 15th March, 1982 P. Greenslade', male, SAMA.

Paratypes

Same data as holotype, 12 males, 4 females, ANIC, SAMA. 'S. Aust. Deep Ck Boat Hbr Lane



FIGURES 7–9. 7, *L. penelopae*, claw segment of metatarsus; 8, ditto, *L. loftyensis*. Scale line 0.25 mm; 9, *L. penelopae*, pygidium of male. Scale line 1 mm.

turnoff pitfalls in heath 1–8 Dec 1983 P. Greenslade', 1 female, SAMA. 'S. AUST. Mt Remarkable NP 11 km SSW Wilmington 32° 44' 56" S 138° 04' 03" E 20–25 Nov 99 pitfall Flinders Ra. MAM00401', 5 females, ANIC, SAMA. 'S. AUS. 11 km SE Whispering Wall (near Para Wirra) 34° 34' 54" S 138° 55' 12" E 27-10-00 SMLR Survey BAR 03201', 17 males, 31 females, SAMA, QMBA, DPIM.

Description

Body uniformly fuscous to piceous, legs rufous. Total length 3.4–5.5 mm, maximum width across elytra 2.3–3.6 mm. *Head* – Surface even, very densely punctate with shallow coarse punctures running together in irregular transverse rows, bearing small recumbent setae. Dorsal part of eye small, slit-like, its maximum width contained about 30 times in interocular distance.

Prothorax – Anterior angles obtuse. Sides of pronotum widest about one-quarter of the distance behind anterior angles, thereafter slightly converging or subparallel to broadly rounded posterior angles. Dorsal surface very densely and uniformly punctate, punctures separated by distances equal to less than their diameter, bearing very fine, short, fully recumbent setae. *Elytra* – Striae very superficial, geminate with slightly crenulate edges, impunctate. Discal intervals flat, in same plane as striae, with more or less undulate surface, finely shagreened, with a row of punctures bearing recumbent setae along edges of each interval, an additional row usually present in middle of intervals near base. *Hind wings* – Atrophied, represented by short stubs. *Sterna* – Mesosternum with shallow punctures on posterior half. Metasternum entirely densely punctate with shallow punctures laterally bearing short, fine recumbent setae. *Legs* – Protibia (Fig. 4) with 3 large teeth on outer edge, which is serrate between teeth and proximal to them. Claws (Fig. 8) strongly dentate. *Abdomen* – Pygidial disc simple, without groove, uniformly densely and shallowly

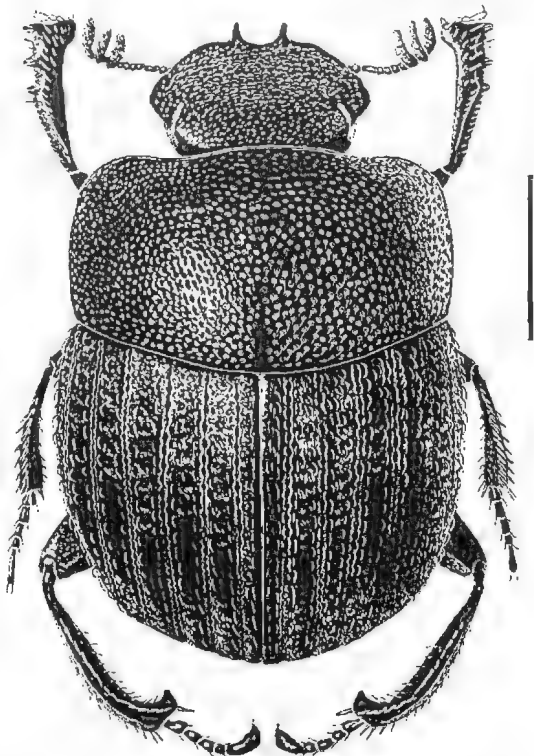


FIGURE 10. *Lepanus loftyensis* male, habitus. Scale line 1 mm.

punctate, punctures bearing very small recumbent setae usually worn off. Aedeagus as in Fig. 11. *Sexual dimorphism* – Male with rounded expansion of inner apical end of protibia bearing apical comb of short, wide, flattened bristles (Fig. 4, c) and a brush of long setae underneath which is directed downward perpendicular to surface. Metatibia of male (Fig. 6) with strongly recurved apical end bearing acute inner tooth. Prothorax of male broader anteriorly, subquadrate; that of female slightly narrower anteriorly. Clypeal teeth of male slightly smaller than those of female.

Remarks

In the key to species of *Lepanus* in Matthews (1974) *L. loftyensis* will first go to couplet 16 because it has three teeth on the outer edge of the protibia, then to couplet 17 because it has a simple pygidium and setose dorsal surfaces, then to *L. villosus* Matthews of north Queensland because of its crenulate elytral striae and densely punctate meso- and metasterna. It differs from *L. villosus* in having superficial elytra striae, reduced hind wings, very different parameres of the aedeagus, and being of much larger size. Further, *L. loftyensis* has the setae on the pronotum only about half the length of those on the elytra, the first elytral interval with a double row of seta-bearing punctures, and the upper edges of the epipleural carina not visible from directly above due to the curvature of the elytra.

The designation MAM 00401 on labels of the Mount Remarkable specimens refers to a locality

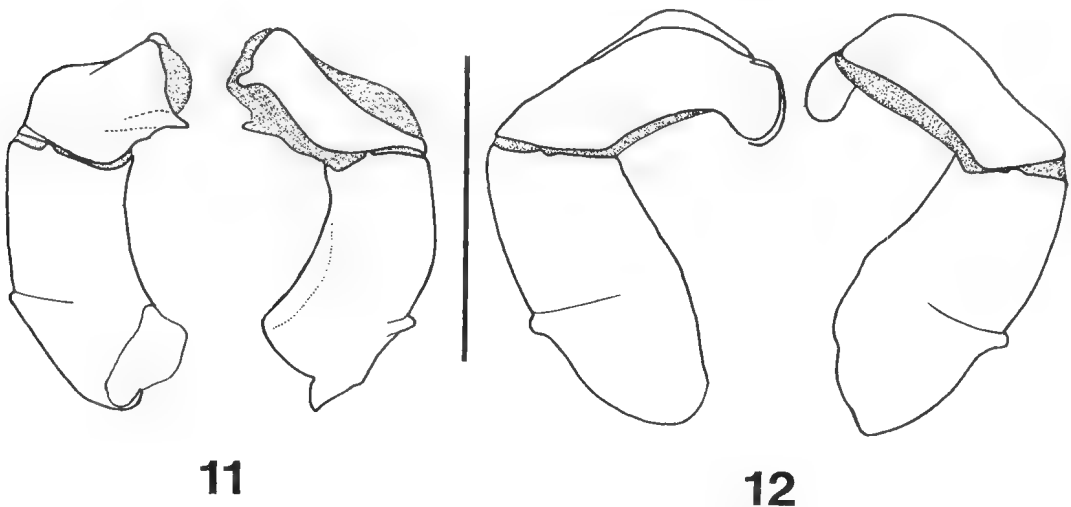
which is described in Brandle (2001) as mountainous, on a hill crest, with loam/sand soil and an overstorey of *Allocasuarina verticillata* at a cover density of 25–50%, and at an altitude above sea level of 430 m. For the Parra Wirra specimens the designation BAR 03201 refers to a ridge top covered with *Eucalyptus fasciculosa* / *Acacia paradoxa* woodland and an understorey of *Calytrix*, *Hakea* and *Xanthorrhoea*, at an altitude of 515 m (L. Queale, pers. comm.).

Etymology

The name refers to the Mount Lofty Block environmental province in which all four collection localities of this species are contained. The block is Province number 3 as delineated in the Biological Survey of South Australia, and extends from Kangaroo Island northward to Mount Remarkable. The biota of this province is characterised as fully Bassian (Brandle 2001).

DISCUSSION

The existence of the species here described as *Lepanus loftyensis* was briefly noted by Matthews (1984: 6, footnote) erroneously as an undescribed species of *Sauvagesinella* Paulian. *Lepanus* and *Sauvagesinella* are closely related genera which are not separable in the female sex, but in the male there are several secondary sexual characters which will distinguish them. Unlike *Lepanus*, *Sauvagesinella* males have a prominent median



FIGURES 11 & 12. Aedeagi in right and left views. 11, *L. loftyensis*; 12, *L. penelopae*. Scale line 1 mm.

tubercle on the metasternum (only a trace of a tubercle in some *Lepanus*), a row of close-set tubercles along the inner edge of the metatibia, and a more or less compressed metafemur with a longitudinal fold or ridge on its ventral surface. *Sauvagesinella* as understood here does not occur outside the extreme southern part of Western Australia, where there are three species (Matthews 1974).

Storey and Monteith (2000) mention that males of all species of *Aptenocanthon* Matthews, where known, have a similar form of the fore tibial apex with its inner angle expanded and bearing a short brush of stiff setae bent downwards at right angles to the upper tibial surface. This is a similar situation to that found in the two species of *Lepanus* described above (eg Fig. 3, b) and is also known to occur in several other species of *Lepanus* and all three species of *Sauvagesinella*. As well as this brush, there is a comb of flattened bristles at the protibial apex (Figs 3 and 4, c)

which occurs, to varying degrees, in all known males of *Aptenocanthon* and *Sauvagesinella* as well as some species of *Lepanus*. Clearly, these male characters are not limited to *Aptenocanthon* but their value in classification must await further studies on the interrelationships of these genera of Scarabaeini, as also pointed out by Storey and Monteith (2000).

In South Australia the only other known representatives of the dung beetle subfamily Scarabaeinae belong to the tribes Onthophagini (native and introduced *Onthophagus* Latreille), Onitini (introduced *Onitis* Fabricius) and Oniticellini (introduced *Euoniticellus* Janssens), none of which make or roll food balls. All these groups are differentiated from the tribe Scarabaeini by their middle and hind tibiae, which are strongly expanded apically. In Scarabaeini these tibiae are slender and only a little expanded, an adaptation for rolling the food material.

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**A CHECKLIST OF CISSEIS (SENSU STRICTO) GORY & LAPORTE, 1839
(COLEOPTERA : BUPRESTIDAE : AGRILINAE)**

SHELLEY BARKER

Summary

A checklist of *Cisseis* (s.s.) Gory & Laporte, 1839 is presented and discussed, summarising the information available on the genus at the present time.

**A CHECKLIST OF *CISSEIS* (*SENSU STRICTO*) GORY & LAPORTE, 1839
(COLEOPTERA: BUPRESTIDAE: AGRILINAE).**

SHELLEY BARKER

BARKER, S. 2002. A checklist of *Cisseis* (*sensu stricto*) Gory & Laporte, 1839 (Coleoptera: Buprestidae: Agrilinae). *Records of the South Australian Museum* 35(1): 85–90.

A checklist of *Cisseis* (*s.s.*) Gory & Laporte, 1839 is presented and discussed, summarising the information available on the genus at the present time.

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MATERIAL

INTRODUCTION

Specimens examined came from the following institutions:

AMSA – Australian Museum, Sydney
ANIC – Australian National Insect Collection, CSIRO, Canberra
BMNH – The Natural History Museum, London
BPBM – B. P. Bishop Museum, Honolulu
HMOE – Hope Museum, Oxford
HUMB – Humboldt University Museum, Berlin
MCSNG – Museo Civico di Storia Naturale Genoa, Italy
MNHN – Museum National d' Histoire Naturelle, Paris
NMVA – National Museum of Victoria, Melbourne
PMCE – National Museum of Czech Republic, Prague
QMBA – Queensland Museum, Brisbane
RMBB – Royal Museum, Brussels
SAMA – South Australian Museum, Adelaide.

Abbreviations:

WA – Western Australia
NWA – Kimberly area, Western Australia
Q – Queensland
NSW – New South Wales
V – Victoria
SA – South Australia
T – Tasmania
NT – Northern Territory.

Many of the Australian buprestid genera have not been reviewed since the death of H. J. Carter in 1941. Because of the large amount of subsequent collecting and confusion with species identification, the genera are in a parlous state of order. One of worst has been *Cisseis* (Coleoptera: Buprestidae: Agrilinae), last researched by Carter (1923, 1929). With the intention of revising *Cisseis*, the author commenced work on the group in 1997. All of the readily available types, more than half of which are housed in European museums, have now been examined. Some of the difficulties have been resolved and a number of new species described (Barker 1998, 1999a, 1999b, 2001). Some species clearly did not belong in *Cisseis* and these, together with nine new species, were placed in a new genus *Stanwatkinsius* Barker & Bellamy (2001). Carter (1923) did not examine male genitalia, which the author has found to be highly diagnostic. As a result, many of his specimens located in various museum collections are incorrectly identified. In order to summarise the knowledge available on the genus, a checklist has been constructed of valid species together with their distributions by state or country. Types and their locations are also listed. The following abbreviations are used: HT = holotype; ST = syntype; LT = lectotype; AT = allotype.

**CHECKLIST OF *CISSEIS* (*SENSU STRICTO*) GORY &
LAPORTE, 1839.**

aberrans Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 98. (♂ HT, Woodridge, WA, H. Demarz, SAMA I 21504). WA.

- acuducta* (Kirby, 1836)(*Trachys*). *Faun. Bor. Amer.*: 162. (♂ HT, N. Scotia, BMNH). Q, NSW, V, SA, T.
- marmorea* (Gory & Laporte, 1839)(*Ethon*). *Mon. Bupr.* ii: 4. (HT, MNHN not seen)
- cuprifrons* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 157. (♂ HT, Australia, Standing, BMNH)
- laeta* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 227. (♂ HT, Australia, Moffarts, BMNH)
- adusta* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 101. (♂ HT, Lucindale, SA, Feueheerdt, SAMA I 21505). SA.
- albertisi* Gestro, 1877. *Ann. Mus. Civ. Stor. Nat. Genova.* 9: 357. (3 ST sex unknown, Somerset, Australia, D'Albertis, 1/75 MCSNG; ♀ ST, Somerset, Australia, RMBB). Q.
- albosparsa* Gory & Laporte, 1839. *Monograph* ii: 3. (HT, MNHN not seen). NT, Q.
- cupriventris* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 161. (♀ HT, Australia, Chevrolat, BMNH).
- inflammata* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 167. (♂ HT, S. Johnstone R., Q, H. W. Brown AMSA K67240) (new syn.).
- aquilonia* Bellamy, 1991. *Tijdschr. v. Ent.* 134: 171. (♂ HT, BPBM not seen). Philippine Arch.
- armstrongi* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 101. (♂ HT, Bogan R., NSW, J. Armstrong, NMVA). NSW.
- augustgoerlingi* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 102. (♂ HT, Marloo Stn., Wurarga, WA, A. Goerling, ANIC). WA.
- aurocyanea* Carter, 1934. *Proc. Linn. Soc. N.S.W.* 59: 258. (♀ HT, Fletcher, Q, E. Sutton, AMSA K67296). NSW, Q.
- bedfordi* Obenberger, 1923. *Casopis Cs. Spol. Entom.* 32: 9. (♀ HT, Cape Bedford, Q, NMPC). Q.
- brooksi* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 102. (♂ HT, Mareeba, Q, J. G. Brooks, ANIC). Q.
- broomensis* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 103. (♂ HT, Broome, WA, H. W. Brown, SAMA I 21509). NWA.
- browni* Carter, 1934. *Proc. Linn. Soc. N.S.W.* 59: 258. (♂ HT, Dedari, WA, H. W. Brown, AMSA K67297). WA.
- carterella* Obenberger, 1935. *Col. Catalogus* 12: 846. (♀ LT, Herberton, Q, C. J. Wild, QMBA)(replac. name). Q.
- elliptica* var. *frontalis* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 170. (homonym).
- carteri* Obenberger, 1924. *Archiv. für Naturg.* 90: 109. (♂ LT, Yilgarn, WA, NMPC). WA.
- chalcophora* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 103. (♂ HT, Kapunda, SA, S. Barker, SAMA I 21507). SA.
- clermonti* Théry, 1945. *Bull. Soc. Ent. Fr.* 50: 46. (HT, MNHN not seen). Bougainville.
- corpulenta* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 104. (♂ HT, Talling stn., Pindar, WA, S. Barker, SAMA I 21511). WA.
- cupreicollis* (Hope, 1846)(*Ethon*). *Ann. Mag. Nat. Hist.* 17: 64. (♂ HT, Moriatta (sic), SA, HMOE no. 893). SA
- aenicollis* (Hope, 1846)(*Ethon*). *Ann. Mag. Nat. Hist.* 17: 65. (♀ HT, Adelaide, HMOE no. 892 2/2).
- cupreola* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 105. (♂ HT, Mt Spec, Q, J. G. B., ANIC). SA, NSW, Q.
- cupripennis* (Guerin, 1836)(*Buprestis*). *Voy. Coquille*: 65. (HT, MNHN not seen). NSW, V.
- semiscabrosa* Thomson, 1879. *Typi Bupr. Mus. Thomson. App.* 1A: 53. (♂ HT, Sydney)(new syn.).
- nitidicollis* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 162. (♂ HT, Australie, Bates, BMNH)(new syn.).
- cyanea* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 105. (♂ HT, Wialki, WA, S. Barker, SAMA I 21512). WA.
- cyaneopyga* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 170. (♀ LT, Lake Austin, WA, H. W. Brown, AMSA K67292). WA.
- goerlingi* Carter, 1936. *Proc. Linn. Soc. N.S.W.* 61: 104. (♀ HT, Marloo stn., Wurarga, WA, A. Goerling, AMSA K67466)(new syn.).
- cyanura* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 163. (2 ♂♂ ST & ♀ ST, BMNH). Q.
- derbyensis* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 106. (♂ HT, Derby, H. W. Brown, SAMA I 21520). NWA.
- duodecimmaculata* (Fabricius, 1801)(*Buprestis*). *Sys. Eleuth.*: 191. (HT sex unknown, BMNH). All mainland states.
- duodecimguttata* (Boisduval, 1835) (*Buprestis*). *Voy. Astrolabe, Entom.* 2: 93. (HT, MNHN not seen).
- quaturodecimnotata* Hope, 1846. *Ann. Mag. Nat. Hist.* 17: 64. (HT not seen, HMOE).
- pustulata* Thomson, 1879. *Typi Bupr. Mus.*

- Thoms. App* 1A: 51. (HT sex unknown, MNHN).
- biologia* Froggatt, 1910. *Australian Insects*: 165. (HT not seen, AMSA?)(new syn.).
- fallaciosula* Obenberger, 1935. *Acta. Soc. Ent. Csl.* 32: 36. (HT sex unknown, PMCE)(new syn.).
- elongatula* Blackburn, 1888. *Proc. Linn. Soc. N.S.W.* 3: 892. (♂ HT, NT, SAMA). NT.
- elliptica* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 170. (♀ LT, Cue, WA, H. W. Brown, NMVA). WA.
- excelsior* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 107. (♂ HT, Mt Carbine, Q, T. M. S. Hanlon & M. Powell, SAMA I 21514). Q.
- ernestadamsi* Barker, 1999. *Rec. S. Aust. Mus.* 32: 46. (♂ HT, Edungalba, Q, E. E. Adams, ANIC). Q.
- fascigera* Obenberger, 1919. *Ent. Mitteilungen* 8: 20. (♂ HT, New Guinea, PMCE no. 23772). New Guinea.
- fraterna* Kerremans, 1900. *Mem. Soc. Ent. Belg.* 7: 80. (♀ HT, Germ. N. G., Webster, BMNH). New Guinea.
- frontalis* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 157. (♂ HT, New Guinée, Standing, BMNH). New Guinea.
- fulgidicollis* Macleay, 1888. *Proc. Linn. Soc. N.S.W.* 3: 1231. (2 ♂♂ ST, Derby, NWA, ANIC). NWA, Q.
- gibbera* (Carter, 1937)(*Neospades*). *Trans. Roy. Soc. S. Aust.* 61: 121. (♀ HT, Mullaly, NSW, H. J. Carter, AMSA K111950). NSW.
- gouldi* (Hope, 1846)(*Ethon*). *Ann. Mag. Nat. Hist.* 17: 65. (♀ HT, Port Essington, HMOE no. 889). NT.
- heroni* Carter, 1934. *Proc. Linn. Soc. N.S.W.* 59: 259. (♂ HT, Dorrigo, NSW, W. Herron, AMSA K67298). NSW.
- impressicollis* Macleay, 1878. *Ent. Soc. N.S.W.* 2: 248. (♀ HT, Gayndah, AMSA K32713). Q.
- viridiaurea* Macleay, 1878. *Ent. Soc. N.S.W.* 2: 248. (2 ♀♀ ST, Gayndah, AMSA no. K32712)(new syn.).
- viridicuprea* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 160. (♀ HT, Cocktown (*sic*), Standing, BMNH)(new syn.).
- nitida* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 164. (♂ HT, Cocktown (*sic*), BMNH)(new syn.).
- inops* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 168. (♀ HT, Australie, Standing, BMNH). NSW.
- kohouti* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 107. (♂ HT, Canberra, K. Pullen, ANIC). NSW, Q.
- laticollis* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 169. (♀ HT, BMNH). Q.
- leucosticta* (Kirby, 1818)(*Buprestis*). *Trans. Ent. Soc. Lond.* 12: 382. (♀ HT, BMNH). All mainland states.
- aurulenta* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 159. (♀ HT, Australia, Chevrolat, BMNH)(new syn.).
- fulgidifrons* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 161. (♀ HT, Australia, Chevrolat, BMNH).
- macmillani* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 108. (♂ HT, Wanneroo, WA, R. P. McMillan, SAMA I 21516). WA.
- macqueeni* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 108. (♂ HT, Milmeran, Q, J. Macqueen, ANIC). Q.
- maculata* (Gory & Laporte, 1839)(*Ethon*). *Mon. Bupr.* ii: 5. (HT, MNHN not seen). NSW.
- marmorata* Gory & Laporte, 1839. *Mon. Bupr.* ii: 4. (HT, MNHN not seen). NSW, Q.
- viridicollis* Thomson, 1879. *Typi Bupr. Mus. Thomson. App.* 1A: 50. (♂ HT, MNHN).
- aena* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 158. (3 ♀♀ ST, Sydney, Bates, BMNH).
- minutissima* Thomson, 1879. *Typi Bupr. Mus. Thomson. App.* 1A: 54. (HT, MNHN not seen). SA, V.
- simplex* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 171. (2 ♂♂ ST & ♀ ST, Australie, Standing, BMNH)(new syn.).
- modesta* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 170. (♂ HT, Australie, Stark, Chevrolat collection, BMNH). WA, SA, V.
- myallae* Carter, 1934. *Proc. Linn. Soc. N.S.W.* 59: 260. (♀ HT, Bogan R., NSW, J. Armstrong, AMSA K67299). NSW.
- nigrita* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 168. (♂ HT, Australie, Fairmaire, BMNH).
- nigripennis* Macleay, 1888. *Proc. Linn. Soc. N.S.W.* 3: 1231. (♂ HT, Barrior (*sic*) Range, NWA, Froggett, ANIC). NT, WA.
- ignicollis* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 164. (♂ ST, Australie, Standing, BMNH; ♂ ST, Australie, Chevrolat, BMNH; 2 ♂♂ ST, Port Denison BMNH)(new syn.).
- nigromaculata* Kerremans, 1895. *Ann. Soc. Ent. Belg.* 39: 218. (HT not in BMNH). Malacca.

- nitidiventris* Carter, 1934. *Proc. Linn. Soc. N.S.W.* 59: 260. (♀ HT, Gosford, NSW, N. MacGregor, AMSA K67300). NSW, Q.
- niveosparsa* (Carter, 1927)(*Neospades*). *Proc. Linn. Soc. N.S.W.* 52: 228. (♂ HT, Bogan R., NSW, J. Armstrong, AMSA K67288). NSW, SA.
- notulata* (Germar, 1848)(*Ethon*). *Linn. Ent.*: 178. (♂ HT, Adelaide, HUMB). SA, NSW, T.
- atroviolacea* Thomson, 1879. *Typi. Bupr. Mus. Thoms. App.* 1A: 52. (♂ ST & ♀ ST, Austr, MNHN)(new syn.).
- morosa* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 158. (2 ♂♂ ST, Australie, Stark, BMNH)(new syn.).
- nubeculosa* (Germar, 1848)(*Ethon*). *Linn. Ent.*: 176. (♀ LT, Adelaide, HUMB). SA, V.
- chalcoptera* (Germar, 1848)(*Ethon*). *Linn. Ent.*: 177. (2 ♂♂ ST, Adelaide, HUMB).
- similis* Saunders, 1871. *Cat. Bupr.*: 103. (♀ HT, Adelaide, BMNH)(new syn.).
- oblonga* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 229. (♀ HT, Australie, Fairm., BMNH). V, NSW, Q, T.
- obscura* Blackburn, 1887. *Trans. R. Soc. S. Aust.* 10: 252. (♀ HT, T 320, type locality unknown, BMNH)(unique).
- opima* Thomson, 1879. *Typi Bupr. Mus. Thomson. App.* 1A: 50. (♀ HT, Champion Bay, MNHN). WA.
- ovalis* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 170. (♀ HT, Nov. Holl. occid., Fry Coll. 1905.100, BMNH 37811)(unique). WA.
- parva* Blackburn, 1887. *Trans. R. Soc. S. Aust.* 10: 253. (♂ HT, BMNH). WA, SA, V, NSW.
- pygmaea* Blackburn, 1891. *Trans. R. Soc. S. Aust.* 14: 299. (♀ HT, Victoria, C. French, NMVA)(new syn.).
- patricia* Carter, 1935. *Proc. Linn. Soc. N.S.W.* 55: 180. (♂ HT, Bunbury, WA, F. L. Whitlock, AMSA K67302). WA, V, NSW.
- pauperula* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 167. (♂ HT, Australie, A. Deyr., Chevrolat collection, BMNH). T.
- prasina* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 168. (♂ LT, Australia, Blackburn's collection, 3267, SAMA). SA, Q.
- puella* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 170. (2 ♂♂ ST & ♀ ST, Australie, Fairm., BMNH). Q.
- curta* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 229. (♂ HT, Peak Downs, Fairmaire, Mus. Godeffroy no. 11142, BMNH).
- pulchella* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 171. (HT sex unknown, French collection, NMVA). Q.
- pulleni* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 109. (♂ HT, Edungalba, Q, S. Barker, SAMA I 21518). ACT, Q.
- regalis* Thomson, 1879. *Typi Bupr. Mus. Thomson. App.* 1A: 50. (♂ HT, Queensland, MNHN). NT, Q.
- robertfisheri* Barker, 1999. *Rec. S. Aust. Mus.* 32: 47. (♂ HT, Melrose, SA, R. H. Fisher, SAMA I 21407). SA.
- roseocuprea* (Hope, 1846)(*Ethon*). *Ann. Mag. Nat. Hist.* 17: 64. (♀ HT, Moriatta (*sic*), SA, HMOE no. 889). WA, SA, V, NSW.
- dispar* Blackburn, 1891. *Trans. R. Soc. S. Aust.* 14: 297. (♀ HT, 3832, BMNH).
- fairmairei* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 169. (♀ HT, Australie, Fairmaire, BMNH).
- cuprea* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 228. (♀ HT, NSW, Standing, BMNH).
- rubicunda* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 169. (♂ HT, Australie, Fairm., BMNH). WA, SA, V, NSW, Q.
- undulata* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 227. (♀ HT, NSW, Standing, BMNH)(new syn.).
- purpurea* Kerremans, 1903. in *Wytzman Genera Ins. fas.* 12: 228. (♀ HT, Sidney (*sic*), Fairm., Mus. Godeffroy no. 11108)(new syn.).
- scabiosa* (Boisduval, 1835)(*Buprestis*). *Voy. Astrolabe Entom.* 2: 96. (HT, MNHN not seen).
- scabrosula* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 167. (3 ♂♂ ST & ♀ ST, Australie, Fairm., BMNH). NSW, Q.
- semiobscura* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 170. (♂ ST, Australie, Fairm., BMNH; 2 ♀♀ ST, Australie, Deyr., BMNH). SA, V.
- septuosa* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 109. (♂ HT, Charity Ck Bridge, Manning R., NSW, S. Watkins, SAMA I 21521). SA, NSW, Q.
- sexnotata* Fauvel, 1891. *Rev. d'Ent.* 10: 181. (HT, MNHN not seen). New Caledonia.
- signaticollis* (Hope, 1846)(*Ethon*). *Ann. Mag. Nat. Hist.* 17: 64. (♂ HT, Port Essington, HMOE no. 891). WA, NT, Q.
- speciosa* Barker, 2001. *Trans. Roy. Soc. S. Aust.*

- 125: 110. (♂ HT, Midland Jctn, WA, R. P. McMillan, SAMA I 21523). WA.
- stellata* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 111. (♂ HT, Cairns, SAMA I 21524). Q.
- stigmata* Gory & Laporte, 1839. *Mon. Bupr.* ii: 3. (HT, MNHN not seen). WA.
- subbifascialis* Carter, 1927. *Proc. Linn. Soc. N.S.W.* 52: 229. (♀ HT, Bogan R., NSW. J. A., AMSA K67291). NSW.
- tasmanica* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 165. (♀ ST, Tasmanie, Oberthur, BMNH; ST, Tasmanie, Chevrolat, BMNH). T, V, NSW.
- trimentula* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 111. (♂ HT, Pilliga East SF, NSW, S. Watkins, SAMA I 21526). V, NSW, Q.
- tyrrhena* Carter, 1923. *Proc. Linn. Soc. N.S.W.* 48: 168. (♀ HT, Kalamunda, WA, H. M. Giles, AMSA K67293). WA.
- vicina* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 164. (♂ HT, Australie, Standing, BMNH). V, NSW, Q.
- collaris* Kerremans, 1903. in Wytsman, *Genera Ins. fas.* 12: 229. (2 ♂♂ ST, Gayndah, Fairmaire, BMNH).
- ornata* Kerremans, 1903. in Wytsman *Genera Ins. fas.* 12: 229. (♂ HT, NSW, Standing, BMNH).
- violacea* Kerremans, 1903. in Wytsman *Gen. Ins. fas.* 12: 228. (♂ ST & ♀ ST, Gayndah, Fairmaire, BMNH). NSW, Q.
- viridiceps* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 168. (♂ HT, Australie, Standing, BMNH). NSW.
- viridipurpurea* Carter, 1924. *Proc. Linn. Soc. N.S.W.* 49: 27. (2 ♂♂ ST, Geraldton, WA, J. Clark, AMSA K67294). WA.
- sapphira* Carter, 1933. *Proc. Linn. Soc. N.S.W.* 58: 163. (♀ HT, Moore R., WA, H. W. B., AMSA K67295)(new syn.).
- watkinsi* Barker, 2001. *Trans. Roy. Soc. S. Aust.* 125: 112. (♂ HT, Tinonee Rd, Manning R., NSW, S. Watkins, SAMA I 21528). NSW.
- westwoodi* (Gory & Laporte, 1839)(*Coraebus*). *Mon. Bupr.* ii: 15. (♂ ST & 2 ♀♀ ST, MNHN). SA, V, T.
- verna* Blackburn, 1891. *Trans. R. Soc. S. Aust.* 14: 299. (HT damaged sex unknown, Warburton District, Victoria, French collection, NMVA).
- viridana* Kerremans, 1898. *Ann. Soc. Ent. Belg.* 42: 165. (♀ HT, Austral., Standing, BMNH).

theryi Kerremans, 1903. in Wytsman *Genera Ins. fas.* 12: 229. (2 ♂♂ ST & 2 ♀♀ ST, Victoria, Théry, BMNH).

DISCUSSION

- C. adspersa* Kerremans (HT not in BMNH) hab. India belongs in another genus.
- C. albertisi* Gestro is not a synonym of *C. acuducta* (Carter 1923) which does not occur at the tip of Cape York in the type locality.
- C. cornuta* Gestro (6 ST, MCSNG) = *Hypocisseis latipennis* Macleay.
- C. duodecimguttata* Guérin-Méneville, 1830 (*Buprestis*). Type species by subsequent designation (Duponchel, 1843).
- C. fossicollis* Kerremans (HT BMNH) = *Alcinous fossicollis* (Kerremans).
- C. fulgidicollis* Macleay is very uncommon in collections and has been confused with other species, particularly with *C. stellata* Barker.
- C. gestroi* Kerremans 1892, *Mem. Soc. Ent. Belg.* 1: 225 is unknown to me; the holotype is not in the BMNH and the species is not listed under *Cisseis* in Kerremans (1903).
- C. maculata* Gory & Laporte was misidentified by Carter (1929) who listed *C. tasmanica* Kerremans and *C. pauperula* Kerremans as its synonyms; both are good species.
- C. modesta* Kerremans was listed as a synonym of *C. rubicunda* Kerremans Carter (1929). I find they are separate species.
- C. nigrita* Kerremans was listed as a synonym of *C. notulata* (Germar) by Carter (1929). Carter (1923) followed Blackburn's concept of *C. notulata*, which was incorrect. *C. nigrita* is a separate species.
- C. nigripennis* Macleay was listed by Carter (1923) as belonging in *Neospades*. I find it belongs in *Cisseis* (s.s.).
- C. obscura* Blackburn is a species that I have been unable to find in any available collection.
- C. ovalis* Carter could be a synonym of *C. opima* Thomson. The unique holotype is a discoloured female specimen.
- C. rugiceps* Thomson belongs in *Neospades*.
- C. scabiosa* (Boisduval) is unknown to me.
- C. semiobscura* Kerremans was listed as a synonym of *C. notulata* by Carter (1929). It is a separate species, much smaller than *C. notulata* and common in South Australia.
- C. spilota* Hope, 1846 (*Ann. Mag. Nat. Hist.* 17: 64) (HT, HMOE not seen) is unknown to me. Hope indicated that it belonged in another

- genus. Carter (1929) incorrectly listed it as a synonym of *C. signaticollis* Hope, 1846; *spilota* has precedence over *signaticollis*.
- C. stigmata* Gory & Laporte, 1839 selected as type species by Bellamy (1998) (invalid).
- C. violacea* Kerremans was listed as a synonym of *C. notulata* by Carter (1929). It is a separate, smaller species occurring in the vicinity of Brisbane, Queensland.

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THE FLORA AND FAUNA OF SOUTH AUSTRALIA HANDBOOKS COMMITTEE 10 MARCH 1921 – 30 OCTOBER 2001

WOLFGANG ZEIDLER

Summary

The Flora and Fauna of South Australia Handbooks Committee has been operating for 80 years producing a series of handbooks on the major elements of the South Australian natural environment. The main role of the Committee was to encourage and persuade specialists to write books on the flora and fauna for no financial reward. The completed manuscripts were then edited by members of the Committee and, in the past, were printed by State Print or its equivalent and published by the State Government Printer at the State Government's expense. Several years ago this part of the Government's operations ceased, with no provision made for the further printing of handbooks.

THE FLORA AND FAUNA OF SOUTH AUSTRALIA HANDBOOKS COMMITTEE
10 MARCH 1921 – 30 OCTOBER 2001

WOLFGANG ZEIDLER

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The Flora and Fauna of South Australia Handbooks Committee has been operating for 80 years producing a series of handbooks on the major elements of the South Australian natural environment. The main role of the Committee was to encourage and persuade specialists to write books on the flora and fauna for no financial reward. The completed manuscripts were then edited by members of the Committee and, in the past, were printed by State Print or its equivalent and published by the State Government Printer at the State Government's expense. Several years ago this part of the Government's operations ceased, with no provision made for the further printing of handbooks.

Since the privatisation of the Government Printer the Committee has sought other means to publish its books and the last two handbooks have been printed with the help of the Board of the Botanic Gardens ('Fungi') and the SA Research & Development Institute (Aquatic Sciences) ('Marine Invertebrates III'). However, it became very clear to the Committee that the only way it could continue was to establish a publications fund.

Initially, the State Government was approached because of its traditional support for the Committee, but this proved fruitless, although the Department of Environment & Heritage and the South Australian Museum did offer some support if funds could also be found from other sources. Various philanthropic trusts were approached and, although some were sympathetic, no funding was forthcoming. Similarly, all three of the State's universities, whose students and staff are amongst the main users of the handbooks, declined to assist. The formation of a partnership with a publisher was also considered, but rejected as it would potentially compromise the original intention of the Committee because handbooks with commercial potential would be favoured.

Left with no alternative, the Handbooks Committee reluctantly concluded that it could not continue to function as originally intended and should be disbanded. The last meeting of the Flora and Fauna of South Australia Handbooks Committee was accordingly held on 30 October 2001.

With the demise of the Handbooks Committee, which was once the envy of all other states, it is important to record its history and major achievements.

The Committee began in 1921 when Prof E. Wood-Jones, Prof T. B. G. Osborn and Prof J. B. Cleland presented the idea to the then Premier Mr H. Barwell. The concept was for authoritative handbooks to be written by experts in their field without remuneration, to be published by the Government Printer at its convenience, and to be sold at a low price so as to be affordable to the wider community. Here follows an extract recording the foundation of the handbooks series, prefacing Eichler's (1965) 'Supplement to J. M. Black's Flora of South Australia'.

After the first World War, the South Australian Branch of the British Science Guild was very active in devising ways for increasing scientific knowledge and its applications. At the time an up-to-date account of the Flora of our State was a pressing need. With this view, Professor J. B. Cleland suggested that the Science Guild might undertake to arrange for the preparation of a series of Handbooks dealing with the Fauna and Flora of South Australia. If these were prepared in an honorary capacity by leading authorities, the Government might well be asked to publish them, as it were, on a pound for pound basis. The Branch accepted the suggestion and it was arranged that a deputation of Professors F. Wood Jones, T. G. B. Osborn and J. B. Cleland should wait on the Hon. The Premier Mr., afterwards Sir Henry Barwell, with the proposal.

Fortunately Professor Cleland had prepared a memorandum on the subject in the following terms and this document was handed to the Premier on 25th February, 1921.

PROPOSED SCHEME FOR THE PREPARATION OF
HANDBOOKS ON THE FAUNA AND FLORA
OF SOUTH AUSTRALIA

- I. There is an almost complete lack in South Australia of any handbooks dealing with the Fauna and Flora of the State.
- II. In consequence, many individuals with scientific tastes are unable to develop these. This is a great loss to the State, as these persons, with suitable handbooks available, might be led on to contribute voluntarily to the State additions to scientific knowledge of great value to our pastoral, agricultural and other interests.
- III. A scheme under the auspices of the S.A. Branch of the British Science Guild is proposed for the preparation of a series of such handbooks to be edited by a sub-committee of experienced workers, the individual parts to be prepared by specialists (in an honorary capacity).
- IX. The scheme would be spread over a period of 10-15 years.
- X. Parts would be issued as completed by the authors. None could be available during this financial year. One or two may be so for 1921-1922.
- XI. The work involved will be highly skilled and laborious. In the interests of science the authors will be prepared, we believe, to devote their time and knowledge to this work without fee, if a means of publication can be obtained.
- XII. The value to the community of the works of these authors, thus offered as a gift to the State and world of science, can be put at a very high figure. Would the Government be prepared to accept this offer of gratuitous service and as a return – on the “pound for pound subsidy” principle – arrange for the publication of the Handbooks by the Government Printer?
- XIII. As the work will be spread over many years, this should not necessitate any additions to the staff of the Government Printer, the printing of the parts being proceeded with by him as opportunity offered. The actual out-of-pocket expense to the State would consist, under these circumstances, of the paper only. The parts as completed might be submitted to

the Premier or to the Minister of Education, and laid on the table of the House and ordered to be printed and thus be dealt with as Parliamentary Papers.

- IX. Many of the parts will require to be illustrated. In many cases, blocks are already prepared which doubtless could be used and so reduce expense.
- X. The educational value of these handbooks will be great. A copy of each might be placed with advantage in every public school in the State, when it could be made available not only to teachers and scholars but to the public of the district as well. To meet this demand and to enable distribution to be made to private individuals (at a nominal price to induce the wide use of these handbooks) about 1,500 copies of each should be printed.
- XI. Probably from 20 to 30 handbooks would eventually be published (over the period of 10-15 years), the sizes varying from about 20 to 150 pages according to subject matter.

Professor CLELAND, Adelaide University.

Professor WOOD JONES, Adelaide University.

The Premier read through the memorandum and said, “A very generous offer, gentlemen. I shall lay it before Cabinet.” Professor Cleland received from the secretary to the Premier, a letter dated 10th March, 1921 in the following terms accepting the offer.

“With reference to the proposed scheme under the auspices of the South Australian Branch of the British Science Guild for the preparation of a series of handbooks on the Fauna and Flora of South Australia which was submitted by yourself and Professor Wood Jones to the Premier on the 25th ultimo, I am directed by the Premier to inform you that in consideration of the contributors in the compilation of the handbooks undertaking the work in an honorary capacity the Government is prepared to undertake the printing of the publication at the Government Printing Office at the expense of the State.”

In recent years the Chief Secretary of South Australia decided that the Government Printer should publish the handbooks on a commercial basis, rather than that the Handbooks Committee should apply each year for a government grant for publication. Consequently there is now no delay in printing when the authors offer their completed manuscripts.

The British Science Guild has long since ceased to exist but the work of the Handbooks Committee survived until now. The main aim of the

Committee has always been to produce books that document, in a rigorously scientific way, the biological heritage of the State, although in recent years the Committee encouraged authors to broaden their focus to southern Australia in general. Perhaps the most outstanding work published by the Committee is the 'Flora of South Australia'. The remarkable J. M. Black produced the four-volume work single-handedly and revised the first three volumes, working until he was 96. Revision of the fourth volume was completed after his death. For South Australia's sesquicentenary a completely revised and rewritten new edition was produced, making this State the only one at the time to have a comprehensive up-to-date record of State flora.

There are also other monumental works for which other states have no equivalent (see list of handbooks) and, while some volumes are out of date, many have been updated or reprinted to meet the demand of scientists, naturalists and students. It seems remarkable that Hale's 'The Crustaceans of South Australia' (1927, 1929), reprinted in 1976, is still used as a basic text, although very much out of date and only providing a limited coverage of the group.

It is clear that the handbooks provide invaluable data for research workers, not only in South Australia, or even nationally, but internationally as well. Indeed, the handbooks series has been the envy of scientists in other states. Their contribution to secondary and tertiary education, as significant textbooks, is well recognised. For example, the four-part 'Flora', 'Fishes' and the three-part 'Marine Invertebrates of Southern Australia' series are essential texts for tertiary students. Unfortunately, the later volumes produced by the Government Printer were managed on a commercial basis and were remaindered within two years, so that they were only available for a relatively short period.

Future plans for new editions of 'Fishes', 'Amphibians', 'The Vegetation of South Australia', 'Crustacea' (as part of the 'Marine Invertebrates' series) and 'Flora' have been abandoned, although they may be taken up by others. In particular, the State Herbarium is in the process of producing an electronic version of the 'Flora', and the South Australian Research & Development Institute (Aquatic Sciences) intends to proceed with future volumes of the 'Marine Invertebrates' series as well as revising earlier volumes.

As part of the winding up process, the Committee has transferred copyright of the botanical texts to the Board of the Botanic Gardens

and State Herbarium, and of the zoological and ecological texts to the Board of the South Australian Museum. Copies of correspondence and minutes of the Handbooks Committee have been deposited with State Archives.

TITLES ISSUED BY THE FLORA AND FAUNA OF SOUTH AUSTRALIA HANDBOOKS COMMITTEE

- 1922 'Flora of South Australia'. Part I. Cyathaceae – Orchidaceae. J. M. Black. Second edition 1943. Reprinted 1948. Reprinted (facsimile) 1960, 1972. Third edition, Lycopodiaceae – Orchidaceae (revised by J. P. Jessop) 1978.
- 1923 'The Fishes of South Australia'. E. R. Waite. Reprinted 1962.
- 1923 'The Mammals of South Australia'. Part I. The Monotremes and the Carnivorous Marsupials. F. Wood-Jones. Reprinted in one volume with parts II (1924) and III (1925), with an Introduction by P. Crowcroft and a Selected Bibliography by J. H. Calaby 1968.
- 1924 'Flora of South Australia'. Part II. Casuarinaceae – Euphorbiaceae. J. M. Black. Second edition 1948. Reprinted 1963. Reprinted (facsimile) 1977.
- 1924 'The Mammals of South Australia'. Part II. The Bandicoots and the Herbivorous Marsupials. F. Wood-Jones. Reprinted in one volume with parts I (1923) and III (1925), as above, 1968.
- 1925 'The Building of Australia and the Succession of Life' with special reference to South Australia. Part I. W. Howchin.
- 1925 'The Mammals of South Australia'. Part III. The Monodelphia. F. Wood-Jones. Reprinted in one volume with parts I (1923) and II (1924), as above, 1968.
- 1926 'Flora of South Australia'. Part III. Meliaceae – Scrophulariaceae. J. M. Black. Second edition, Callitrichaceae – Plumbaginaceae 1952. Reprinted 1964. Reprinted (facsimile) 1977.
- 1927 'The Crustaceans of South Australia'. Part I. H. M. Hale. Reprinted in one volume with part II (1929) 1976.

- 1928 'The Building of Australia and the Succession of Life' with special reference to South Australia. Part II. Mesozoic and Cainozoic. W. Howchin.
- 1929 'Flora of South Australia'. Part IV. Bignoniaceae – Compositae. J. M. Black. Second edition, Oleaceae – Compositae (revised by E. L. Robertson) 1957. Reprinted (facsimile) 1980.
- 1929 'The Crustaceans of South Australia'. Part II. H. M. Hale. Reprinted in one volume with part I (1927) 1976.
- 1929 'The Reptiles and Amphibians of South Australia'. E. R. Waite.
- 1930 'The Building of Australia and the Succession of Life' with special reference to South Australia. Part III. Pleistocene. W. Howchin.
- 1934 'Toadstools and Mushrooms and other Larger Fungi of South Australia.' General introduction; Toadstools and Mushrooms. J. B. Cleland. Reprinted in one volume with part II (1935), including 'Notes on some Edible and Poisonous Fungi' by P. H. B. Talbot, 1976.
- 1935 'Toadstools and Mushrooms and other Larger Fungi of South Australia'. Polypores, Coral Fungi and remaining Hymenomycetes; Puff-balls, Jelly-like fungi, the larger Ascomycetes and Myxomycetes. J. B. Cleland. Reprinted in one volume with part I (1934), as above.
- 1936 'The Seaweeds of South Australia'. Part I. Introduction and The Green and Brown Seaweeds. A. H. S. Lucas.
- 1937 'The Vegetation of South Australia'. J. G. Wood.
- 1938 'The Molluscs of South Australia'. Part I. The Pelecypoda. B. C. Cotton & F. K. Godfrey.
- 1939 'Primitive Insects of South Australia'. Silverfish, Springtails and their allies. H. Womersley.
- 1940 'The Molluscs of South Australia'. Part II. Scaphopoda, Cephalopoda, Aplacophora and Crepidopoda. B. C. Cotton & F. K. Godfrey.
- 1947 'The Seaweeds of South Australia'. Part II. The Red Seaweeds. A. H. S. Lucas & F. Perrin.
- 1959 'South Australian Mollusca'. Archaeogastropoda. B. C. Cotton.
- 1961 'South Australian Mollusca'. Pelecypoda. B. C. Cotton.
- 1962 'The Marine and Freshwater Fishes of South Australia'. T. D. Scott.
- 1964 'South Australian Mollusca'. Chitons. B. C. Cotton.
- 1965 'Supplement to J. M. Black's Flora of South Australia' (second edition 1943–1957). H. J. Eichler.
- 1966 'Aboriginal Man in South and Central Australia'. Part I. Edited by B. C. Cotton. Only one part was published.
- 1972 'The Vegetation of South Australia'. R. L. Specht. Second edition.
- 1974 'The Marine and Freshwater Fishes of South Australia'. T. D. Scott, C. J. M. Glover & R. V. Southcott. Second edition. Reprinted (facsimile, with 16 pp of colour plates) 1980.
- 1975 'Plant Feeding and other Bugs (Hemiptera) of South Australia'. Heteroptera Part I. G. F. Gross.
- 1976 'Plant Feeding and other Bugs (Hemiptera) of South Australia'. Heteroptera Part II. G. F. Gross.
- 1978 'Butterflies of South Australia'. R. H. Fisher.
- 1978 'Amphibians of South Australia'. M. J. Tyler.
- 1979 'Lichens of South Australia'. R. B. Filson & R. W. Rogers.
- 1980 'Mosses of South Australia'. D. G. Catcheside.
- 1980 'Acacias of South Australia'. D. J. E. Whibley.
- 1982 'Marine Invertebrates of Southern Australia'. Part I. Edited by S. A. Shepherd & I. M. Thomas.
- 1984 'Pysilloidea of South Australia'. F. D. Morgan.
- 1984 'The Marine Benthic Flora of Southern Australia'. Part I. H. B. S. Womersley.
- 1986 'The Dynamic Partnership: Birds and Plants in Southern Australia'. Edited by H. A. Ford & D. Paton.

- 1986 'Flora of South Australia. Volumes I-IV'. Edited by J. P. Jessop & H. R. Toelken. Fourth edition (third edition consisted of part I only).
- 1986 'The Ecology of Forests and Woodlands of South Australia'. Edited by H. R. Wallace.
- 1987 'The Marine Benthic Flora of Southern Australia'. Part II. H. B. S. Womersley.
- 1989 'Marine Invertebrates of Southern Australia'. Part II. Edited by S. A. Shepherd & I. M. Thomas.
- 1990 'Orchids of South Australia'. R. Bates & J. Z. Weber.
- 1992 'Acacias of South Australia'. D. J. E. Whibley & D. E. Symon. Second edition.
- 1994 'The Fishes of Australia's South Coast'. Edited by M. F. Gomon, J. C. M. Glover & R. Kuitert.
- 1997 'Larger Fungi of South Australia'. C. A. Grgurinovic.
- 1997 'Marine Invertebrates of Southern Australia'. Part III. Edited by S. A. Shepherd & M. Davies.

Dr Wolfgang Zeidler (Hon. Secretary), on behalf of the Flora and Fauna of South Australia Handbooks Committee — Em Prof William D. Williams (Chairman), Dr Sue Barker (Botanical Editor), Dr Margaret Davies (Zoological Editor), Dr Shelley Barker, Ms Robyn Barker, Dr John G. Conran, Mr Peter Copley and Dr Brian D. Morley.

OBITUARY GRAEME LLOYD PRETTY 1940 – 2000

HELEN TOLCHER

Summary

Graeme Lloyd Pretty was born in Melbourne on 25 June 1940. His father was in the RAAF and the family soon moved to Richmond NSW, where Graeme spent his childhood and went to school. After graduating from Sydney University BA (Hons) in Classical Archaeology and Dip Ed, he contemplated undertaking a PhD with Jack Golson at the Australian National University. However, he began working at the South Australian Museum in January 1962 as Assistant Curator of Anthropology under Norman Tindale, from whom he learned much and with whom he kept in touch long after the latter's retirement. His first interest was in Melanesian prehistory – he might well have made this his major field of work.

OBITUARY

GRAEME LLOYD PRETTY

1940–2000



Graeme Pretty and Henry Pollach (left) at Roonka, 8 August 1971.
Roonka photos R83: 2. South Australian Museum.

Graeme Lloyd Pretty was born in Melbourne on 25 June 1940. His father was in the RAAF and the family soon moved to Richmond NSW, where Graeme spent his childhood and went to school. After graduating from Sydney University with a BA (Hons) in Classical Archaeology and Dip Ed, he contemplated undertaking a PhD with Jack Golson at the Australian National University. However, he began working at the South Australian Museum in January 1962 as Assistant Curator of Anthropology under Norman Tindale, from whom he learned much and with whom he kept in touch long after the latter's retirement. His first interest was in Melanesian prehistory—he might well have made this his major field of work.

In 1964 he was appointed Assistant Curator of Archaeology, and archaeological fieldwork was added to his duties. He excavated or assisted at a number of sites on the lower River Murray, seeking the advice of John Mulvaney who had recently excavated Fromm's landing. At the same time he continued research into

Melanesian culture, including six weeks fieldwork in the Southern Highlands of Papua New Guinea (PNG) in 1968–69. Subsequently, he was invited to review the functions of the PNG Museum and Art Gallery. Later, he also advised the Australian National Gallery on its Melanesian collections.

In 1968 Pretty began a project that was to become the most important one of his working life. A salvage operation to remove a surface campsite and scattered human remains from a sandhill beside the River Murray at Roonka, near Blanchetown, developed into a major excavation that would attract worldwide interest. At that time he was unique in having consulted with the relevant Aboriginal group and obtained approval before beginning work—he continued this contact throughout and after the conclusion of the dig. This rapport with the Aboriginal people undoubtedly contributed to making possible the excavation on the scale and significance that was achieved.

Despite the disadvantages and difficulties of working on a surface fully exposed to gale-force winds and summer heat rising to the 50°C range, he retrieved a wealth of archaeological material and information from a site which proved to have been occupied for some 18 000 years. In all, 216 complete or fragmentary burials were uncovered. The grave goods were unprecedented at that time. In addition to almost every variant of human mortuary practice, it also gave evidence for hitherto undocumented customs, of which there were well over 150 examples.

Roonka looms large for its deep significance. Here is a statistical sample from one place, across some thousands of years, permitting health, injury and dietary studies of the population. Pretty correctly saw that aspects of the rituals involved—the mode of burial, including grave goods, and the antiquity of the rituals—presented a major window to past belief and behavioural systems. No other burial ground has produced so much evidence.

The almost exclusively amateur workforce of volunteers became, over the eight years of active fieldwork, a team of patient, dedicated, highly skilled excavators. Under Pretty's direction, the site was strictly controlled, meticulously recorded and kept secure from outside interference. The standard and scope of the work attracted substantial financial support as well as visitors from abroad, including osteo-archaeologists and a delegation from the People's Republic of China. One group will remember the visit not only for the archaeology but because their bus became bogged to the axles on the Roonka Flat.

Pretty was appointed to the position of Senior Curator of Anthropology and Archaeology in 1975.

The section of Pretty's work that has been best documented is probably that dealing with chronology. He had a critical appreciation of the role of physical dating methods in archaeology and sought to create a temporal framework for the finds at Roonka. The chronology of the site was determined by a larger number of different dating methods than any other archaeological site in Australia, including thermoluminescence, palaeomagnetism, uranium fluorimetry and C-14 dating, both conventional and AMS.

It is not generally known that he was responsible for planting the idea for developing luminescence dating in the Physics Department at the University of Adelaide in conversation with Professor John Prescott. This was in 1972, at the very infancy of the thermoluminescence

technique. The earliest Adelaide work on thermoluminescence dating *per se* was based on samples from Roonka.

Pretty extended his fieldwork research to Island Melanesia in 1971 and 1973, finding additional support from sources outside Australia. However, the demands of attempting to elucidate the intricacies of the Roonka information, together with constraints on finance and staffing, resulted in the Melanesian work being put aside—apart from ongoing work, under his direction, on the sorting of the Foreign Ethnology reserve collections and their eventual rehousing at Kent Town in 1986. As Senior Curator of Archaeology, Pretty's work was directed almost exclusively to organising the mass of information from the Roonka site in order to arrive at what he considered an adequate assessment on which to base his final report. During the 1980s a master index of the Roonka data was prepared.

The Third Australasian Archaeometry Conference was held in Adelaide in 1988. Pretty devised the theme of the Symposium, 'Early Man in the Southern Hemisphere', which was designed to give a specifically archaeological balance to the program. He arranged invitations and finance for the international contributors: G. Delibrias, G. J. Bartstra and H. J. Deacon; and organised the conference excursion and wrote the field notes.

In his own contribution to the symposium, a paper analysing the cultural chronology of Roonka, it is possible to see a foretaste of his overall interpretation of Roonka in its wider context. An early indication is also found in his exciting and innovative 1977 paper, 'The cultural chronology of Roonka Flat'. In it he remarked 'This present paper therefore celebrates the author's satisfaction that the archaeology is now sufficiently clear to commit preliminary notice of it to paper'. Yet, during the following 23 years, he produced no paper with the promised detail. It is difficult for those of us who knew him to avoid reflection on his apparent reluctance to put his ideas on paper where they could be exposed to the critical appraisal of his peers. He did publish sections of the work with his collaborators, but the overall synthesis was yet to come. Perhaps he was sensitive to possible criticism; perhaps the very volume of his material was an obstacle. It seems likely that he laboured over the precise language with which to present a polished final monograph.

In 1982 restructuring of the South Australian Museum's divisions and staffing made Pretty one of a number of Curators of Anthropology. He

accepted a severance package in 1994, continuing his work on the Roonka report until 1996, when he was stricken with viral encephalitis, from which he never fully recovered. He died on 6 November 2000.

In his work Pretty was patient, a seeker of precision in language that was baffling to many, and single-minded to a degree that ignored workplace relationships and, at times, made it difficult for people to work with him. His memory was exceptional. The breadth of his reading was remarkable and was reflected in his large personal library. He left the Museum's Foreign Ethnology collection well organised and totally accessible, and the Roonka material fully recorded and stored. He gained the respect of his field workers, instructing them in aspects of Aboriginal culture and inspiring in them a dedication and loyalty to the project that will ensure the publication of the final report.

Graeme married Dana in 1973 and they had one daughter. To those who knew him well he was a kind and considerate friend. At home he was a gracious and amusing host, an erudite and entertaining conversationalist, a devoted husband and a proud and loving father.

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PRETTY, G. L. 1968. Excavation of Aboriginal graves at Gidgealpa, South Australia. *Records of the South Australian Museum* 15, 4: 671–677.

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- The following are in manuscript form and it is intended that they will be published in due course.**
- PRETTY, G. L. 'Archaeological Investigations at Roonka, Part I - Description of the evidence gathered from the Karmakalingbila Ngaiawang territory: Geological and geochronological background; cultural landscape and stratification; ecological, demographic and cultural finds'. Text, tables, illus.
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- PRETTY, G. L. 'Archaeological Investigations at Roonka, Part 3 - Ethnoductive and systemic analysis: Conjectures about the mechanics and dynamics of cultural change in the Karmakalingbila Ngaiawang territory in the light of its Central Southern Australian context'. Text, tables, illus.
- PRETTY, G. L. 'Archaeological Investigations at Roonka, Part 4 - Decoding the symbol inventory of the Karmakalingbila Ngaiawang sequence: Restoring immediate intelligibility and ultimate causal identity to culturally unfamiliar modes of action through appeals to phyletic behavioural repertoires'. Text, tables, illus.
- PRETTY, G. L. 'Archaeological Investigations at Roonka, Part 5 - The explanation of prehistoric hunter-gatherer culture change in the Karmakalingbila Ngaiawang territory during the Holocene; tests of confirmation and concluding synthesis'. Text, tables, illus.
- Art**
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- No. 2 PRETTY, G. L. 'The National Folk Province Concept - Specification for a feasibility study'.
- No. 3 ROWNEY, B. G. 'Kapunda - Historical development of its town plan'.
- No. 4 PRETTY, G. L. 'The National Folk Province Concept and the National Estate'.
- No. 5 KALIBATAS, E. 'Craigie's Plains: Construction and materials analysis of a historic vernacular sheep station'.
- No. 8 SPIERS, G. K. 'Survey of Heritage Agencies in South Australia'.
- No. 9 ROWNEY, B. G. 'Surviving cottages in Mine Square, Kapunda'.
- No. 10 PRETTY, G. L. (with B. G. ROWNEY & P. F. DONOVAN). 'Ngaiawang Folk Province: Preliminary inventory of the cultural landscape'.
- No. 11 SPIERS, G. K. 'The administration of heritage properties through Local Government: I, The South Australian Planning and Development Act 1996-1975'.
- No. 12 DONOVAN, P. F. & SCHEPPERS, K. H. 'Report on the Kapunda Colonial Festival, 1976'.
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THE LARVAE OF SOME AUSTRALIAN AQUATIC HYDROPHILIDAE (COLEOPTERA : INSECTA)

C. H. S. WATTS

Summary

The larvae of the aquatic Hydrophilid genera *Allocotocerus* Kraatz, *Hydrogralius* Orchymont and *Regimbartia* Zaitzev are described and figured for the first time. The larvae of the following Australian species are also described and figured, most for the first time: *Allocotocerus punctatus* (Blackburn); *Amphiops aueenslandicus* Balfour-Browne; *Berosus australiae* Mulsant; *Enochrus eyrensis* (Blackburn), *E. mastersi* (W. MacLeay); *Helochares tristis* (W. MacLeay), *H. clypeatus* (Blackburn), *H. tenuistriatus* Regimbart, *H. foveicollis* (Montrouzier); *Hydrobiomorpha* sp. ; *Hydrophilus bilineatus* (MacLeay); *Hydrogralius hartmeyer* (Regimbart); *Laccobius decipiens* Gentili; *Limnoxenus zealandicus* (Broun); *Regimbartia attenuata* (Fabricius); and *Sternolophus marginicollis* (Hope).

THE LARVAE OF SOME AUSTRALIAN AQUATIC HYDROPHILIDAE (COLEOPTERA: INSECTA)

CHS WATTS

WATTS, CHS. 2002. The larvae of some Australian aquatic Hydrophilidae (Coleoptera: Insecta). *Records of the South Australian Museum* 35(2): 105–138.

The larvae of the aquatic Hydrophilid genera *Allocotocerus* Kraatz, *Hybograllius* Orchymont and *Regimbartia* Zaitzev are described and figured for the first time. The larvae of the following Australian species are also described and figured, most for the first time: *Allocotocerus punctatus* (Blackburn); *Amphiops queenslandicus* Balfour-Browne; *Berosus australiae* Mulsant; *Enochrus eyrensis* (Blackburn), *E. mastersi* (W. MacLeay); *Helochaeres tristis* (W. MacLeay), *H. luridus* (W. MacLeay), *H. clypeatus* (Blackburn), *H. tenuistriatus* Regimbart, *H. foveicollis* (Montrouzier); *Hydrobiomorpha* sp.; *Hydrophilus bilineatus* (MacLeay); *Hybograllius hartmeyer* (Regimbart); *Laccobius decipiens* Gentili; *Limnoxenus zealandicus* (Broun); *Regimbartia attenuata* (Fabricius); and *Sternolophus marginicollis* (Hope).

The larvae were identified by rearing larvae collected in the field, or occasionally by association and elimination, or by using biochemical methods.

The pupae of *Amphiops queenslandicus* and *Hybograllius hartmeyer* are described and figured. Unlike most other Hydrophilids the larvae of *Amphiops* are thought to pupate exposed on the stems of emergent vegetation.

A key is provided to the larvae of Australian genera of aquatic Hydrophilids other than *Notohydrus* Balfour-Browne, *Paranacaena* Blackburn, *Phelea* Hanson and *Agraphydrus* Regimbart, whose larvae remain unknown.

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Manuscript received 23 April 2001.

The Hydrophilidae (sensu Hansen 1991) comprise a major part of the Australian aquatic beetle fauna, occurring in all types of fresh water and most commonly among vegetation at the edge of standing water. Adults and larvae occur together. The taxonomy of the adults is now relatively well known thanks to the work of Hansen (1991) at the generic level and above; and that of Gentili (1980, 1992, 1993, 2000) and Watts (1987, 1988, 1989, 1990, 1995, 1998a, 1998b) on the aquatic fauna at the species level. No recent work has been done on the species level taxonomy of the extensive portion of the family in which both adults and larvae are terrestrial.

In contrast to the situation with adults, the only work specifically on Australian larvae is that of Anderson (1976) who described the larvae of *Helochaeres tristis* (W. MacLeay), *Enochrus maculiceps* (W. MacLeay) and *Chasmogenus nitescens* (Fauvel) together with details of their life histories.

One feature of the Australian aquatic Hydrophilid fauna is its low endemism at the generic level. Consequently, descriptions of a

number of Australian genera are available in scattered Northern Hemisphere publications. The work on the New World genera was summarised and added to by Archangelsky (1997). This work included a number of genera which also occur in Australia.

For a number of years I have been rearing field-collected larvae of Australian aquatic Hydrophilids with the aim of discovering and describing the larvae of all genera and, for those already known from non-Australian species, to extend the descriptions to incorporate Australian species. The basic motivation was to produce a key to enable the larvae of all Australian aquatic Hydrophilidae to be identified at least to genus. As a result I have reared 12 species in 9 genera. Two additional genera, *Allocotocerus* and *Regimbartia*, were identified by associating adults and larvae by the biochemical technique of alloenzyme electrophoresis. Others were identified using the descriptions in Archangelsky (1997), eg *Hydrobiomorpha*; or by association and elimination, eg *Enochrus mastersi*.

I have not attempted any phylogenetic analysis

since, with such a high proportion of genera also occurring widely outside Australia, the only sensible approach would have been to include an examination of all known genera, which was beyond the scope of this study. Some comments on relationships are given under most generic descriptions.

In preparing this paper I have drawn heavily on the work of Archangelsky (1997) on the New World fauna. The descriptions follow his format and a number of the figures used to illustrate the key come from his important publication.

Although their larvae are known from other places, I have not seen Australian examples of the following genera: *Chaetarthria* Stephens, *Chasmogenus* Sharp, *Crenitis* Bedel, *Coelostoma* Brulle or *Paracymus* Thomson, and since I have nothing to add have not included descriptions. Detailed descriptions can be found in Archangelsky (1997). In addition, the larvae of *Paranacaena* Blackburn, *Notohydrus* Balfour-Browne, *Phelea* Hanson and *Agraphydrus* Regimbart are unknown.

MATERIALS AND METHODS

Larvae were collected in the field and reared in small aquaria formed by placing the base of a small petrie-dish inside a larger petrie-dish and filling the space between them with damp sand (Watts 1963). Mosquito and chironomid larvae were the main food items provided. These were accepted by all larvae other than those of *Hydrophilus* (see under *Hydrophilus*). All species successfully reared pupated in cells constructed in the wet sand with the exception of those of *Amphiops* which pupated on the surface or attached to the sides of the container.

Larvae were preserved in 75% ethanol and examined under a stereomicroscope. Permanent microscope slides were prepared for detailed examination. Drawings were made with the aid of a camera lucida. Habitus drawings were only prepared when no previous illustration was available or when Australian species differed from those previously illustrated. Unless otherwise mentioned the descriptions are based on third instar larvae. Earlier instars usually differ somewhat, most noticeably in the stouter cephalic appendages and in fewer spines on the mentum. The key is constructed to accommodate all instars. Measurements of the head capsule were made under a stereoscopic microscope with a graduated eyepiece. Measurements of total

length were made with dial callipers on both mounted and alcohol preserved material, but in this case the measurements can only be indicative as factors such as larval age and preservation effects can alter the length considerably. Measurements of the head capsule, particularly the width, are a more reliable indicator of size. Unless stated otherwise, the specimens were collected by myself and are in the collection of the South Australian Museum.

SYSTEMATICS

KEY TO THE GENERA OF AUSTRALIAN AQUATIC HYDROPHILIDAE BASED ON LARVAL CHARACTERS

- 1) Not including the genera *Notohydrus*, *Paranacaena*, *Phelea* and *Agraphydrus*, whose larvae are not known.
- 2) Including *Spercheus* which is in the family Spercheidae but which has larvae that can be confused with Hydrophilidae.
 - 1 — Tip of mandible bifid (Fig. 2g)
..... Spercheidae (*Spercheus*)
 - Tip of mandible not bifid
..... Hydrophilidae...2
- 2 — Hypopharyngeal lobe well developed, like a pubescent tongue, originating at the base of the labium on the left side (Figs 2a, 2b)
Subfamily Sphaeridiinae*
..... *Coelostoma* Brulle
 - Hypopharyngeal lobe reduced or absent
..... Subfamily Hydrophilinae...3
- 3 — Abdominal segments with long filamentous gills (Fig. 5a), or with multiple setose lateral projections on abdominal and thoracic segments (Fig. 15a)
..... Tribe Berosini...4
 - Lacking long filamentous abdominal gills or complex lateral projections, at most with simple short fleshy projections (Figs 4a, 14a, 16a) 6
- 4 — Gills long, without setae (Fig. 5a); labroclypeus asymmetric (Fig. 5b); mandibles asymmetric (Fig. 5f); prementum small and squat, without ligula (Fig. 5c), basal segment of antenna without lateral projection (Fig. 5e)
..... *Berosus* Leach
 - Abdominal and thoracic segments each with two or more setose, lateral projections

- (Fig. 15a); mandibles nearly symmetrical (Fig. 15h); prementum long and thin, with ligula (Fig. 15d); basal segment of antenna with lateral projection (Fig. 15g) 5
- 5 — Body spines predominantly blunt, weakly bifid at tips (Fig. 3b); lateral projection on basal segment of antenna near apex, sharp, spine-like (Fig. 3f); apex of second segment of antenna with lateral extension (Fig. 3d); maxillary stipe without spines (Fig. 3e); ligula relatively short, prementum stouter (Fig. 3c) *Allocotocerus* Kraatz
- Body spines predominantly pointed (Fig. 15c); lateral projection on basal segment of antenna thumb-like, further from apex (Fig. 15g), second segment of antenna without lateral extension (Fig. 15e); maxillary stipe with spines on inside (Fig. 15f); ligula relatively long, prementum more elongate (Fig. 15d) *Regimbartia* Zaitzev
- 6 — Apical segment of antenna about same length as penultimate (Figs 12d, 16e); femora with fringe of swimming-hairs (Fig. 2h); with prostyles (two retractable, fleshy appendages on last abdominal segment) Subtribe *Hydrophilina*... 7
- Apical segment of antenna much shorter than penultimate (Figs 9e, 14e); femora lacking, or virtually lacking, swimming-hairs; without prostyles 9
- 7 — Labroclypeus without teeth (Fig. 12a); mandibles asymmetrical, left one very robust, right one more slender (Fig. 12e); ligula shorter than first segment of labial palpus (Fig. 12b); up to 40 mm long *Hydrophilus* Muller
- Labroclypeus with weak to moderate teeth (old specimens may lack teeth due to wear) (Figs 11e, 16f); mandibles symmetrical or nearly so; ligula longer than first segment of labial palpus (Figs 11b, 16c); up to 20 mm long 8
- 8 — Prementum longer than mentum (Fig. 16c); first segment of antennae with few spines (Fig. 16f); mandibles each with two large distal teeth and one small proximal denticle (Fig. 16f) *Sternolophus* Solier
- Prementum slightly shorter than mentum (Fig. 11b); first segment of antenna with numerous spines on inside (Fig. 11c); mandibles each with one large distal tooth which is pick-shaped at the tip and one or two small proximal denticles (Fig. 11e) *Hydrobiomorpha* Blackburn
- 9 — Left expansion of epistoma much more prominent than the right and with a row of stout setae on front edge (Fig. 13b); left mandible with group of stout setae at base of middle tooth which is lacking on the right mandible (Fig. 13f) 10
- Lateral expansions of epistoma similar, without a row of stout setae on front edge (Fig. 14b); mandibles without such a group of setae 11
- 10 — Frontal sulci parallel and not uniting to form a coronal sulcus (Fig. 13a); nasale with three teeth (Fig. 13b); prementum wider than long (Fig. 13c); ligula absent or virtually so (Fig. 13c) *Laccobius* Erichson
- Frontal sulci meet just before occipital foramen to form a coronal sulcus (Fig. 10a); nasale with five teeth (Fig. 10b); prementum longer than wide (Fig. 10c); ligula present though small (Fig. 10c) .. *Hybograllus* Orchymont
- 11 — Legs very short, without claws, prementum with a large round ligula (Fig. 2e); length up to 6 mm *Chaetarthria* Stephens
- Legs usually longer, with claws. Prementum with or without ligula, but if present never large and round; length up to 15 mm 12
- 12 — Mentum large, wider than long, prementum small, lacking ligula (Fig. 4b) *Amphiops* Erichson
- Mentum square or longer than wide, prementum well developed, ligula present (Figs 6b, 8b, 14c) 13
- 13 — All abdominal segments with dorsal sclerites, although often small; without coronal sulcus (Fig. 2c); length up to 6 mm; antennal appendage as long as apical segment; mandibles symmetrical with three teeth Tribe *Anacaenini*... 14
- Abdominal segments, other than 1 and 8, lacking dorsal sclerites; with short coronal sulcus (Fig. 1a); antennal appendage half length of apical segment (Fig. 8d); mandibles often asymmetrical and with fewer than three teeth; length up to 15 mm 15
- 14 — With lateral abdominal flaps (Fig. 2c); without cervical sclerites *Crenitis* Bedel

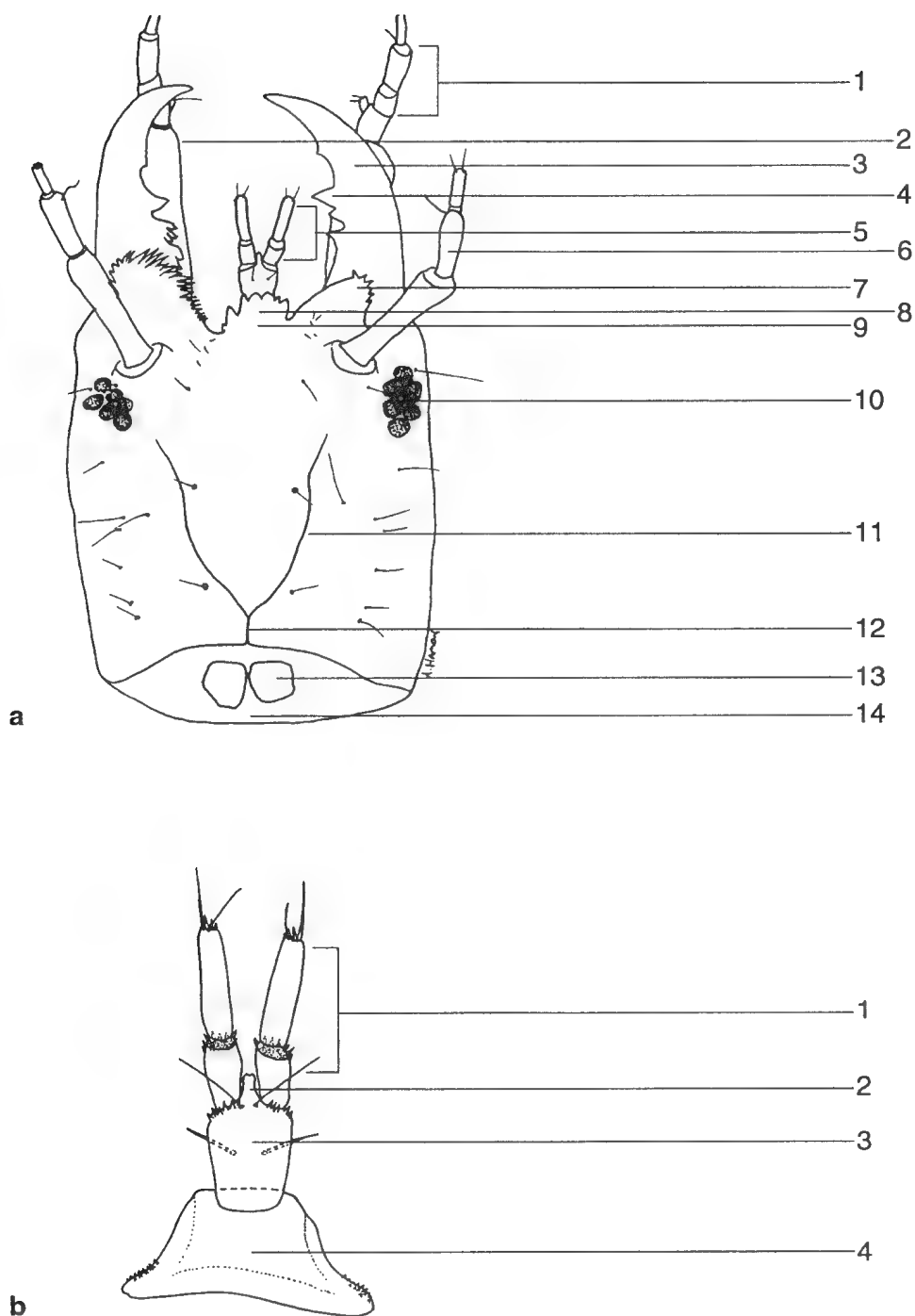


FIGURE 1. **a**, dorsal side of head capsule of *Hybograllius hartmeyer*. 1, maxillary palpus; 2, stipes of maxillary palpus; 3, mandible; 4, mandibular teeth; 5, labium; 6, antenna; 7, right lobe of epistome; 8, teeth of nasale; 9, nasale (7 & 9 make up the labroclypeus); 10, stemmata; 11, frontal sulci; 12, coronal sulcus; 13, cervical sclerites; 14, occipital foramen; **b**, details of dorsal side of labium of *Hybograllius hartmeyer*. 1, labial palpus; 2, ligula; 3, prementum; 4, mentum.

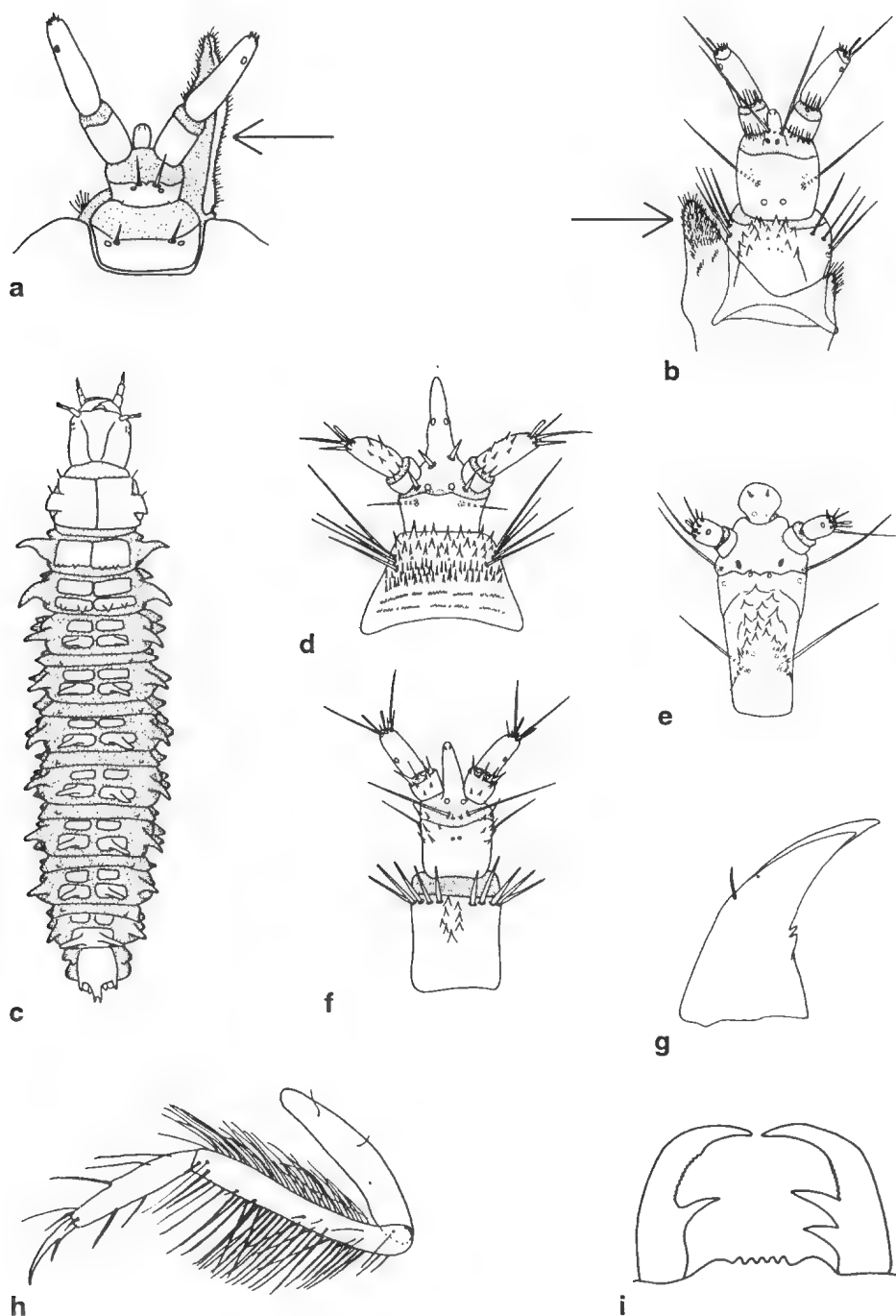


FIGURE 2. a, ventral view of labium and hypopharyngeal lobe (arrowed) of *Sphaeridium scarabaeoides* (Linnaeus) (subfamily Sphaeridiinae); b, dorsal view of labium and hypopharyngeal lobe (arrowed) of *Dactylosternum* sp. (subfamily Sphaeridiinae); c, habitus of *Crenitis morata* (Horn); d, ditto, dorsal view of labium; e, ditto of *Chaetarthria* sp.; f, ditto, *Paracymus subcupreus* (Say); g, mandible of *Spercheus platycephalus* MacLeay; h, hindleg of *Hydrobiomorpha* sp., Northern Territory; i, labroclypeus and mandible of *Chasmogenus nitescens* (Fauvel). a–f, North American taxa from Archangelsky 1997; i, from Anderson 1976.

- Lacking abdominal flaps; with small cervical sclerites . *Paracymus* Thomson
- 15 — Apical segment of antenna about half length of penultimate (Fig. 14e); mandibles symmetrical with three teeth, without serrations (Fig. 14f) *Limnoxenus* Motschulsky
- Apical segment of antenna about a quarter the length of the penultimate segment (Fig. 8d); mandibles weakly to strongly asymmetric, with one or two teeth, often with serrations (Figs 6e, 8e) Subtribe Acidocerenia....16
- 16 — Nasale moderately developed, with right side more prominent (Fig. 6a) 17
- Nasale poorly developed, all areas equally prominent (Fig. 9b) 19
- 17 — Mandibles asymmetric, the right one with one tooth, left with two (Fig. 6e) *Enochrus* Thomson (other than *E. mastersi*)
- Mandibles almost symmetrical, both with two teeth (Fig. 8e) 18
- 18 — Inside of maxillary stipe with group of spines near base (Fig. 8c); ligula longer than first segment of labial palpus (Fig. 8b); prementum approximately the same length as mentum (Fig. 8b)....*Helochares* Mulsant (other than *H. foveicollis*)
- Inside of maxillary stipe lacking such spines (Fig. 7c); ligula shorter than first segment of labial palpus (Fig. 7b); prementum approximately twice length of mentum (Fig. 7b) *E. mastersi* (W. MacLeay)
- 19 — First segment of antenna with bulge on inside near apex (Fig. 9e); mandibles each with two teeth (Fig. 8f) *H. foveicollis* (Montrouzier)
- First segment of antenna without bulge; right mandible with one tooth, left one with two (Fig. 2i) *Chasmogenus* Sharp

* Members of the subfamily Sphaeridiinae are predominantly terrestrial, occurring in moist situations such as dung and rotting vegetation. Members of only one genus, *Coelostoma*, are commonly found in aquatic situations in Australia.

DESCRIPTIONS

The following descriptions are arranged in alphabetic order of the genera.

Allocotocerus Kraatz

Allocotocerus punctatus (Blackburn) Fig. 3

Size of third instar. Length 8.5–12.0 mm; head capsule, 0.70–1.00 mm long, 0.85–1.0 mm wide.

Head capsule. Subquadrangular, bulging outwards at anterolateral angles. Labroclypeus symmetrical; nasale very short, with numerous very short teeth on anterior border of epistome; lateral lobes of epistome rounded, very short. Frontal sulci straight, reaching from antennal bases to rear of head. Coronal sulcus absent. Gular sclerite absent. Cervical sclerites small, subrectangular, very weakly sclerotised.

Antennae. Three-segmented. First segment slender, longer than other two combined, with a spine-like inner process close to apex; third antennal segment short, connected to edge of the second segment before apex. Sensory appendage on second segment, slim, shorter than third segment.

Mandibles. Symmetrical, long and slender, with two inner teeth on basal half; distal tooth large, basal one small.

Maxillae. Five-segmented. Stipes slender, much longer than remaining segments combined, with two or three fine setae on inner margin. Palpus four-segmented; first and third segments subequal in length, first segment bearing a short inner process; second segment very short; fourth segment shorter than third.

Labium. Mentum large, subglobular, dorsal surface with some cuticular spines towards sides, anterolateral angles rounded with a few spines. Prementum much longer and narrower than mentum, subrectangular, longer than wide. Palpus two-segmented, basal segment short. Ligula about two times as long as basal segment of palpus, tip broadened.

Thorax and legs. Prothorax with broad dorsal sclerite, with sagittal line, surface covered by minute spines, fringe of long, slender setae around the margins and three short setae-bearing projections at sides; ventral surface with large, subrectangular sclerite, without sagittal line. Mesothorax with two dorsal pairs of subtriangular sclerites. Metathorax with one dorsal pair of irregular shaped sclerites. Both mesothorax and

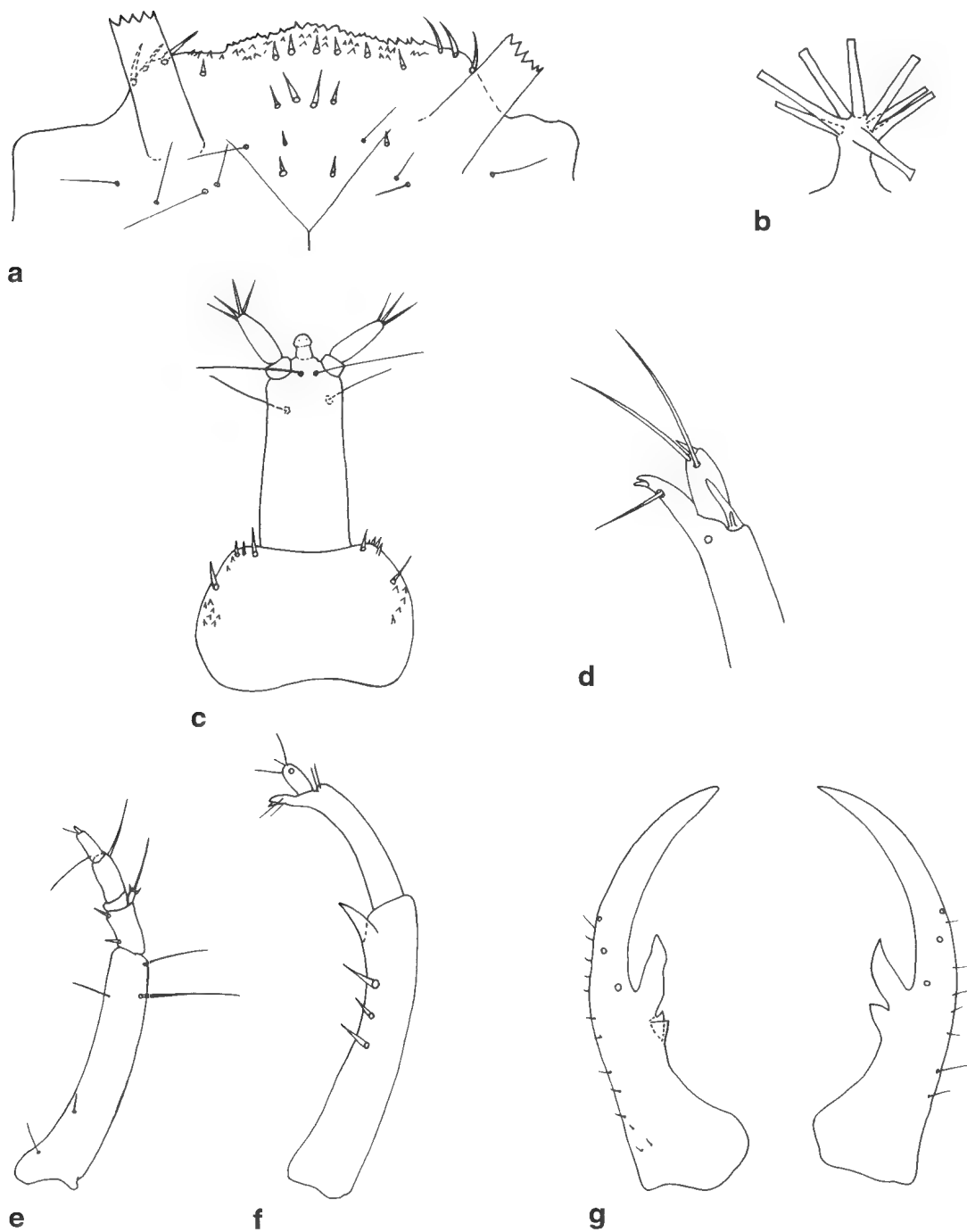


FIGURE 3. *Allocotocerus punctatus*. a, labroclypeus; b, detail of abdominal stella; c, labium; d, tip of antenna; e, maxilla; f, antenna; g, mandibles.

metathorax with three lateral pairs of setiferous projections and a number of short setiferous papillae on dorsal surface. Legs five-segmented, long, visible from above.

Abdomen. Segments 1 to 7 with four pairs of setiferous projections similar to those on thorax, three on the side and a smaller dorsal one towards the midline. In addition, the abdomen is covered with minute, simple spines and the dorsal surface with small projections, each with six to eight, relatively long setae, truncated or weakly bifid at tips (in most specimens these structures are obscured by an accumulation of sand grains and detritus). Segment 8 without setiferous projections; with dorsal semispherical sclerite covering the spiracular atrium; with a pair of small finger-like 'procerci'. Segment 9 trilobed, with a pair of small, unsegmented urogomphi.

Spiracles. Mesothorax and abdominal segment 2 with pair of small non-functional spiracles on short papillae. (I have been unable to detect spiracles on other abdominal segments.) Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Interspecific variation

There is little variation among the few specimens seen — including one from the Northern Territory which is almost certainly *A. tibialis* (Balfour-Browne).

Identification

By association of adult and larva by isoenzyme electrophoresis.

Remarks

The larvae closely resemble those of the New World genus *Derallus* (Archangelsky 1997; Spangler 1966) in the setiferous body structures, form of the labroclypeus, mandibles, labium, maxillary palpi and antennae. The differences are small: blunt rather than sharp-pointed body spines, shape of the distal part of the antennae, number of spines on the maxillary palpi and details of the labium. The larva of *Allocotocerus* is also closely similar to those of *Regimbartia*, differing from this genus in the details of the same suite of characters. On balance it more closely resembles *Derallus*. Although placed by Hansen (1991) with *Berosus* in the tribe Berosini, on larval characters the three genera form a very distinctive and cohesive group well separated from *Berosus*, a conclusion reached by others (Bertrand 1972; Oliva 1992; Spangler 1966).

Specimens examined

Queensland: 2 km S Mt Molloy, 30/3/96. *Allocotocerus* sp. **Northern Territory:** Manton Dam, 23/3/98.

Amphiops Erichson

Amphiops queenslandicus Balfour-Browne. Figs 4, 17a

Size of third instar. Length 6.5–9.0 mm; head capsule 0.65–0.80 mm long, 0.78–0.82 mm wide.

Head capsule. Subquadrate. Labroclypeus symmetrical; nasale very short, with five small teeth; lateral lobes of epistome rounded, projecting further than nasale. Frontal sulci inversely bell-shaped, meeting before reaching occipital foramen. Coronal sulci very short. Gular sclerite absent. Cervical sclerites small, rectangular.

Antennae. Three-segmented. First segment as long as second; third half the length of second. Sensory appendage on second segment short, a quarter the length of the third segment.

Mandibles. Symmetrical with three inner teeth, the two distal teeth large and with slightly crotchet-shaped tips; third tooth much smaller.

Maxillae. Five-segmented. Stipes narrow, longer than the remaining segments combined, with a row of five to six small setae on inner margin. Palpus four-segmented; first segment elongate, rectangular, with inner process as long as very short second segment; third segment longer and narrower than first; fourth segment a little longer than second.

Labium. Mentum large, subrectangular, anterior edge with five to six large spines/protuberances, and numerous cuticular spines at sides towards base. Prementum ovoid, much smaller than submentum. Palpus short, two-segmented, basal very short, distal segment two to three times longer than basal one. Ligula absent.

Thorax and legs. Pro-, meso- and metasterna, almost completely covered by dorsal sclerites, each with a sagittal line. Ventral surface of prothorax with a subrectangular sclerite, subdivided by a sagittal line. Sclerites with very small spines arranged in short lines towards rear (only visible under high magnification). Bases of setae on sclerites pigmented. Legs five-segmented, moderately developed, visible in dorsal view. Dorsal surface with sparse covering of small dark patches.

Abdomen. First segment with dorsal pair of

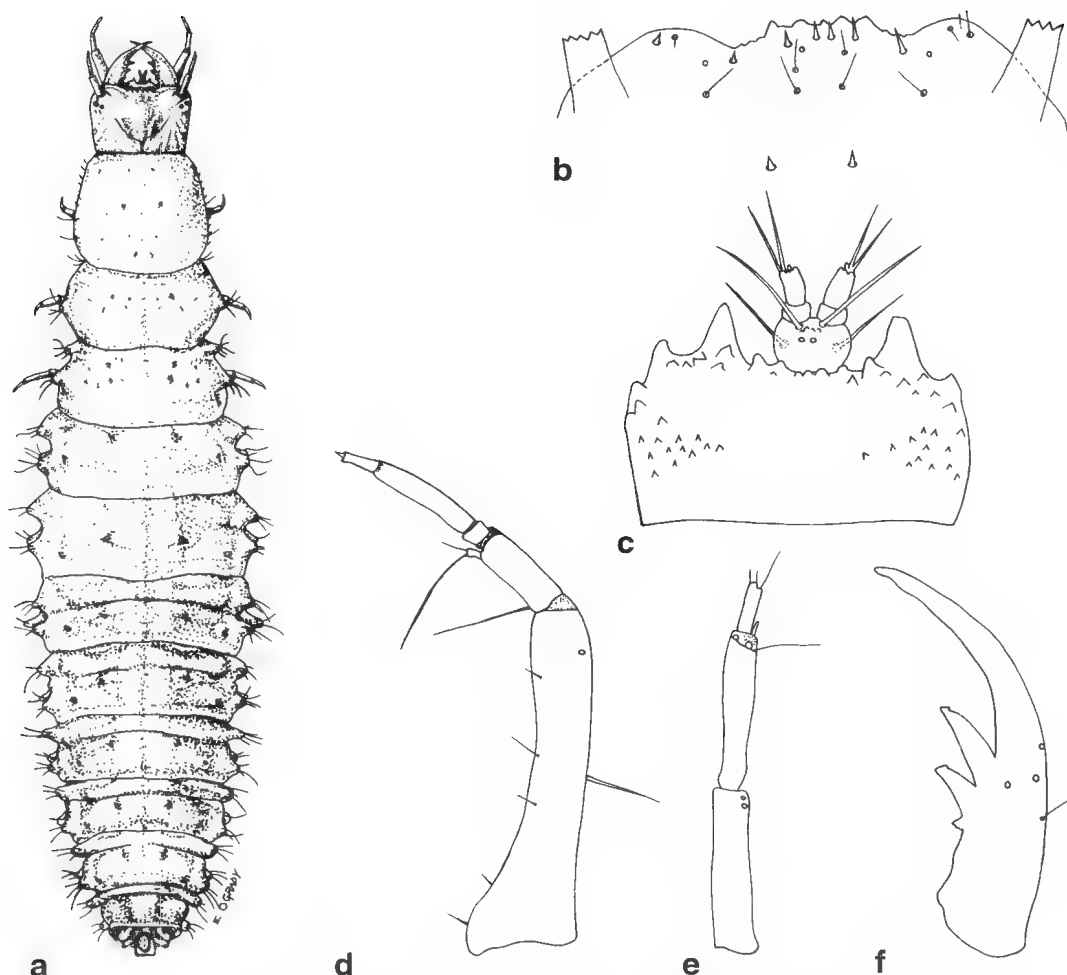


FIGURE 4. *Amphiops queenslandicus*. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandible.

moderate sized subtriangular sclerites, segments 2 to 5 with smaller dorsal sclerites, sclerites with scattered small darker patches. Segments 1 to 7 similar in size and shape, subdivided by a transverse fold; pleural areas with four pairs of moderate bulges/lobes each with several long setae at apex, ventral one largest; with a pair of small dorsal papillae, each with long terminal setae, abdominal surface strongly folded. Segment 8 with pair of small 'procerci', with a large dorsal, suboval sclerite; segment 9 trilobed, with a pair of small one-segmented urogomphi. Integument with only a few small spines.

Spiracles. Eight abdominal pairs; pairs 1 to 7 non-functional, on tips of small papillae and each with a

long seta immediately inwards on a small cylinder-shaped base. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Pupa. (Fig. 17a)

Colour. Light to dark brown.

Head. With one pair of supraorbital styli; styli without apical setae. Appendages adpressed tightly to body, weakly differentiated externally.

Thorax. Pronotum with 16 styli, all on margins of pronotum. Mesothorax lacking obvious styli; metanotum with two pairs of styli, lateral ones near the base of wingpads very small, central pair prominent. Styli without setae. Wing cases grooved/ridged. Legs held tightly against body almost totally covered by pterothecae.

Abdomen. Segments 1 to 7 with a transverse row of four to five very small tergal styli on a sharp ridge that is stronger laterally. Segments 1 to 7 with well-developed rigid flap-like lateral extensions, those on segments 1 to 3 upright and slightly bent over inwards, those on segments 4 to 7 horizontal and each with a small stylus on posterior edge, each stylus with a small seta. Anterior edge of first tergite with very prominent, thin, rigid ridge. Segment 8 without obvious styli; segment 9 bearing a pair of medium-sized cerci.

Interspecific variation

There is little variation among the specimens of *Amphiops* available, although it is almost certain that several species are included. There are some differences, namely: the extent of the dorsal small dark patches/spots varies from a few to moderate numbers; the area between the abdominal sclerites and spiracles sometimes is a bit darker than rest; and there is some variation in the width of the nasale.

Identification

By rearing larvae collected in the field.

Remarks

Bertrand (1972) keyed out *Amphiops* larvae and briefly illustrated a presumed larva. Australian species appear to have less well-developed lateral abdominal protuberances than the specimen from the Indonesian Archipelago (Insulinde) illustrated by Bertrand (1972). Berge Henegouwen (1982) described an African species as having short conical outgrowths.

The noticeably lumpy sides to the abdomen, the very small prementum and labial palpi, and the lack of a ligula most readily identify specimens of *Amphiops*.

The form of the pupae is unusual, in particular the virtual absence of setae, the compact ventral surface and hard shield-like dorsal surface.

In the laboratory *A. queenslandicus* (and also *A. duplopunctatus*, of which a single larva was reared through to adult but the larval exuvium was lost) pupated above ground in the aquaria. This, together with the unusual shape and dark colour of the pupae, suggest that in the wild they pupate attached to the stems of emergent vegetation. Just how they physically attach themselves remains to be discovered.

Specimens examined

Queensland: 1 km W Mingela, 4/5/98.

Amphiops sp. **Northern Territory:** Jabiru,

21/3/98; 11 km E Jabiru, 19/3/98; Manton Dam, 23/3/98; Ormiston Gorge, 27/1/99. **Queensland:** 10 km S Cardwell, 7/2/97; 40 km S Cardwell, 7/2/97; 5 km NE Mt Molloy, 30/3/96; 2 km S Mt Molloy 30/3/96; Nardello's Lagoon near Mareeba, 29/3/96; same locality, 6/2/97; 10 km W Petrie, 23/11/95; 12 km NW Townsville, 8/2/97; 25 km S Townsville, 25/3/96.

Berosus Leach

Berosus australiae Mulsant. Fig. 5

Size of third instar. Length 6.5–1.05 mm (exclusive of gills); head capsule 0.75–0.95 mm long, 0.85–1.02 mm wide.

Head capsule. Subquadrate. Labroclypeus strongly asymmetrical; nasale narrow, strongly protruding, left of centre, with five to seven short teeth; lateral lobes of epistome asymmetrical, right one weakly projecting, left one strongly projected anteriorly, covering basal third of mandible, with several short, strong, curved spines. Frontal sulci lyrriform, not coming together; absent on third instar larvae. Coronal sulcus absent. Gular sclerites absent, a pair of small, weakly sclerotised, cervical sclerites. With inverted U-shaped darker markings on dorsal surface.

Antennae. Three-segmented, relatively close together, arising just inwards of mandible bases. First segment a little longer than other two combined, with a stout subapical seta on inner margin. Sensory appendage on second segment, about half length of short third segment.

Mandibles. Slender, strongly asymmetrical; right mandible with large distal tooth and a very small central one; left mandible with group of seven small teeth or strong spines, some of which are bifid at tips.

Maxillae. Five-segmented. Stipes much longer than remaining segments combined, with four or five setae on inner margin. Palpus four-segmented; first segment short, subquadrate, with an inner process; second segment very short; third segment the longest; fourth a little longer than first.

Labium. Mentum short, poorly sclerotised. Prementum small, subquadrate. Palpus long, two-segmented, basal segment shorter than distal. Ligula absent or reduced to small bulge.

Thorax and legs. Prothorax with large dorsal sclerite, with sagittal line; ventral surface with a large subrectangular sclerite, hind edge strongly sinuate, with sagittal line. Mesothorax with two

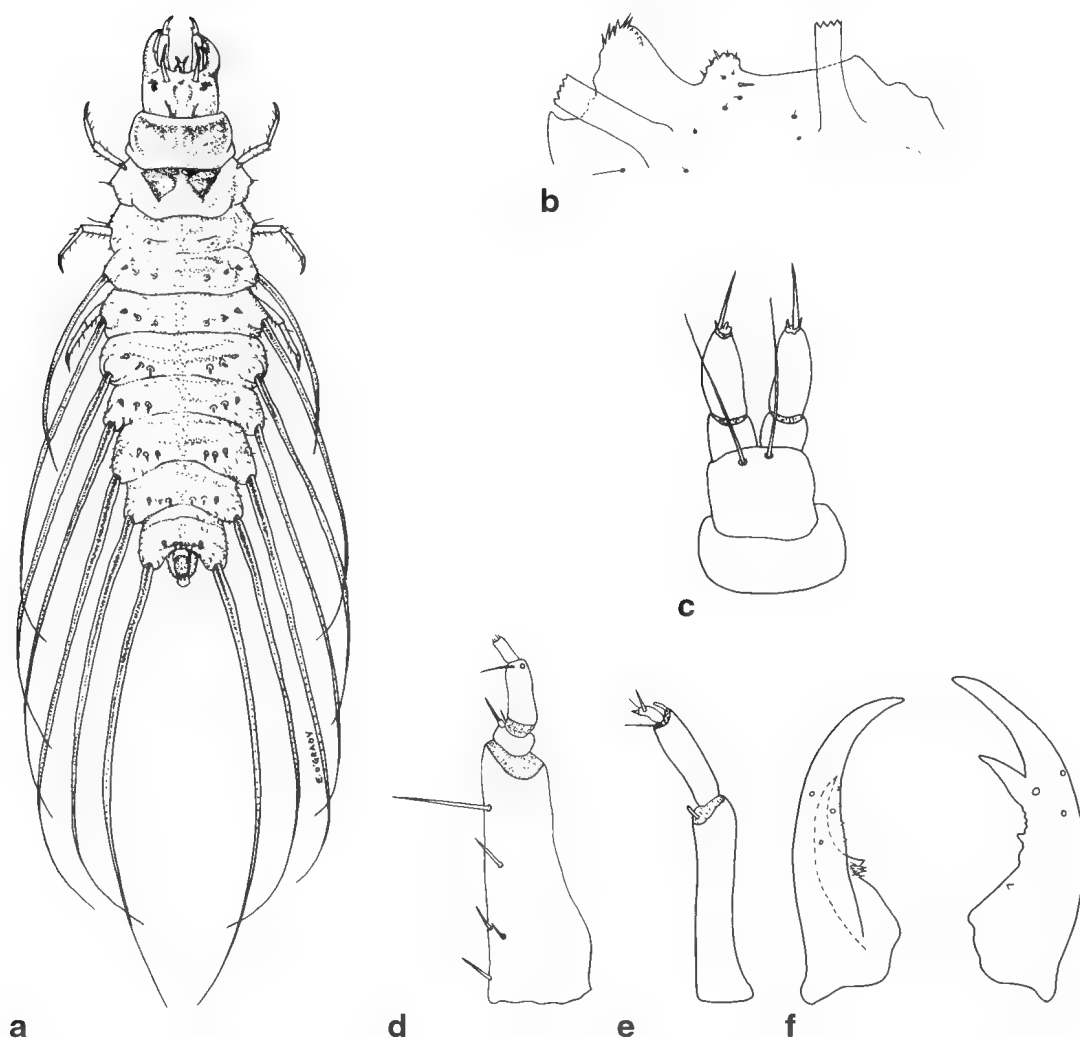


FIGURE 5. *Berosus australiae*. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandibles.

dorsal pairs of sclerites, inner pair small, outer pair much larger, subtriangular. Metathorax lacking sclerites. Mesothorax and metathorax with a pair of small lateral tubercles bearing a long apical seta. Legs five-segmented, long, visible in dorsal view.

Abdomen. Abdominal segments 1 to 7 subdivided by a transverse fold; each with a pair of long, lateral, tracheal gills, and two pairs of small cylindrical structures on dorsal surface in a line inward from spiracles. Segment 8 small, with a dorsal sclerite; spiracular atrium absent. Urogomphi reduced. Integument densely covered

with small setae. Bases of gills with covering of small setae similar to those on adjacent abdominal segments. Each gill with a relatively long seta, arising from a small cylindrical base, towards tip. Dorsal surface often with darker patterning.

Spiracles. Nine pairs of non-functional spiracles, one mesothoracic and eight abdominal.

Intraspecific variation

There is some variation in the specimens I have identified as this species in the number and shape of the nasale teeth and in the presence/absence/strength of a dorsal colour pattern.

Interspecific variation

The description of *B. australiae* fits most of the specimens of *Berosus* that I have seen, many of which are unlikely to be *B. australiae*. I suspect that the description would fit the larvae of most species in the *B. australiae*, *B. majusculus* Blackburn, *B. veronicae* Watts group of Australian *Berosus*. There is some variation in colour and in the strength of setae on the integument (weak in *B. australiae*). Another group of specimens show clear differences from *B. australiae*: the nasale is central rather than to the left; the integument is covered with small dark-pigmented patches in various patterns; the abdominal segments have variably sized, but often marked, colour pattern; there are finger-like projections on the sides of the prothorax and a differently shaped eighth abdominal segment. These larvae are associated with species such as *B. queenslandicus* Blackburn and *B. involutus* (W. MacLeay).

Identification

By association and elimination.

Remarks

The long filamentous lateral gills and the absence of functional spiracles readily identify larvae of *Berosus*. The asymmetry of the mandibles and labroclypeus, stout maxillae and lack of a ligula are also distinctive, but are characters shared variously by a number of other genera. Within Australian species there is no sign of the variation in the number of pairs of lateral gills seen in African (Bertrand 1972) and New World (Archangelsky 1997) species.

Specimens examined

Queensland: Bohle River, 10 km N Townsville, 23/3/96.

Berosus sp. **New South Wales:** 8 km N Bombala, 28/11/98; ditto, 3/11/97; Collector, 20/1/97; 5 km NE Dartmoor, 11/10/96. **Northern Territory:** Mt Borradaile Station, 26/5/99; Nawurlandja, Kakadu National Park, 29/1/99. **Queensland:** Burdekin River, 2/11/95; 10 K S Cardwell, 7/2/97; Jourama Falls, 31/10/95; 5 km NE Mt Molloy, 30/3/96. **South Australia:** 10 km N Coonawarra; 19/10/99. **Victoria:** Simpson Creek, 12 km SW Orbost, 16/1/97. **Western Australia:** Gin Gin, 15/10/96; 4 km S New Norcia, 15/10/96.

Enochrus Thomson

Enochrus eyrensis (Blackburn). Fig. 6

Size of third instar. Length 9.1 mm; head capsule 0.70–0.75 mm long; 0.75–0.80 mm wide.

Head capsule. Subquadrate. Labroclypeus asymmetrical; nasale obliquely truncate, left side shorter than right, with seven to nine short teeth, first two on right side and last one on left side largest; left lobe of epistome rounded, shorter than nasale; right lobe triangular, sharply pointed, about same length as nasale. Frontal sulci as an inverted bell, fusing just before reaching occipital foramen. Coronal sulcus very short. Gular sclerite absent. Cervical sclerites moderate, subrectangular.

Antennae. Three-segmented. In third instar first segment wider than second segment and about same length; second segment with small setae-bearing appendage on inside near middle; third segment about a third the length of the second. Sensory appendage on second segment much shorter than third segment.

Mandibles. Strongly asymmetrical; right mandible with two strong inner teeth on basal half; left mandible with one strong inner tooth. Inner margin of right distal tooth and distal parts of both mandibles serrated.

Maxillae. Five-segmented. Stipes wide, much longer than remaining segments combined, with four strong setae on inner margin. Palpus four-segmented; first segment subrectangular, a little wider than long, with an inner process a little shorter than second palpal segment; second segment short; third and fourth segments about twice as long as second, subequal in length.

Labium. Mentum subtrapezoidal, dorsal surface with two short stout spines in middle towards front, three strong spines laterally, anteriolateral angles each with a strong spine. Prementum squat, a little wider at base, shorter than mentum. Palpus two-segmented, first segment short, second segment approximately twice as long as first. Ligula slender, longer than first palpal segment, with partial ring of small spines around bases of palpal segments.

Thorax and legs. Prothorax completely covered by a dorsal sclerite, with sagittal line; two small very narrow sclerites on rear edge; front half of ventral surface with large sclerite with sagittal line. Mesothorax with large rectangular dorsal sclerite with sagittal line, with numerous strong setae; anterior half of metathorax with dorsal sclerite with sagittal line, posterior half with two

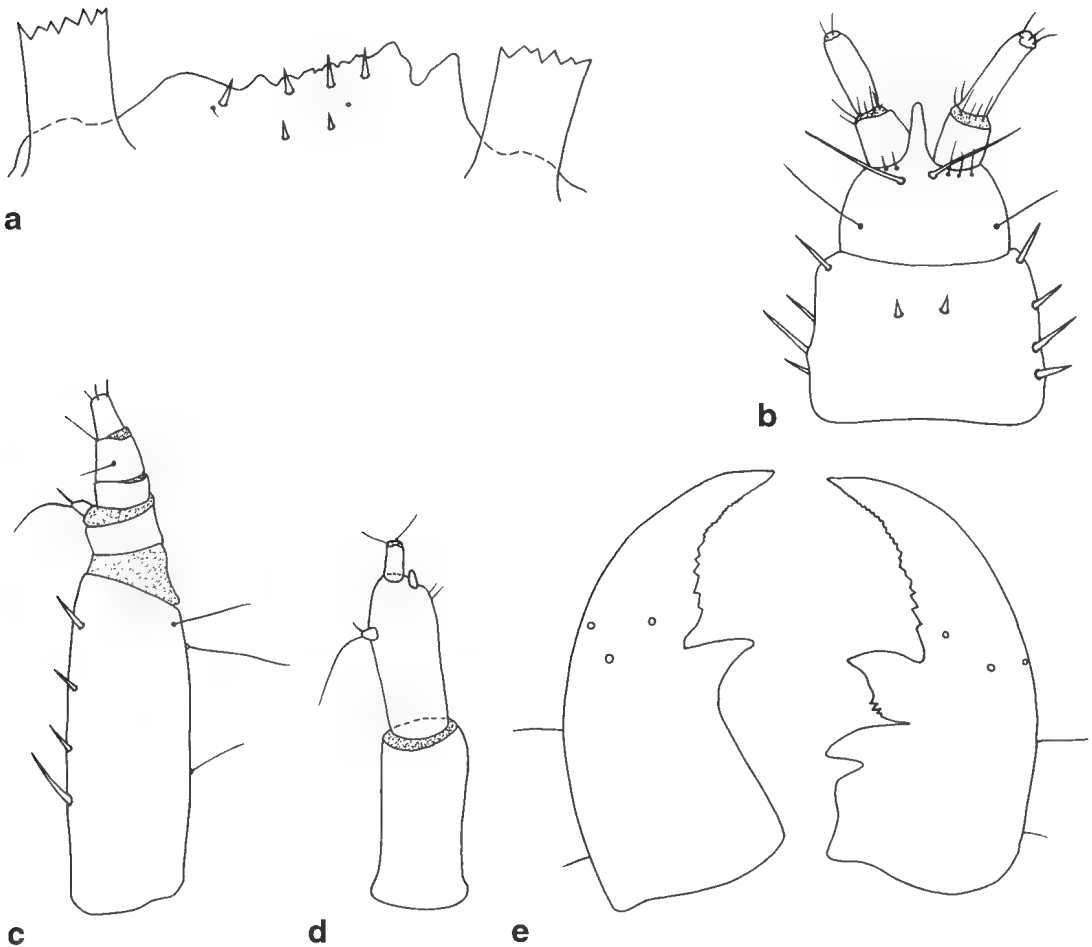


FIGURE 6. *Enochrus eyrensis*. a, labroclypeus; b, labium; c, maxilla; d, antenna e, mandibles.

small foot-shaped sclerites. Legs five-segmented, well developed, visible in dorsal view.

Abdomen. Segments 1 to 7 similar in shape and size, subdivided into three or four transverse folds; segment 1 with two dorsal pairs of small suboval sclerites, the anterior pair much the smaller. Segment 8 with a large, suboval, dorsal sclerite. Segment 9 trilobed, with a pair of short one-segmented urogomphi. Segments 2 to 7 with ventral pair of small protuberances covered with relatively strong, hooked setae (prolegs). Integument rather sparsely covered with small setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional. Spiracles on

segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

No significant variation within the few specimens seen.

Interspecific variation

Within the few specimens available, which must include at least two additional species, there is some variation in the distribution of setae on the thoracic sclerites, in the number and relative size of the nasale teeth, and in the length of the ligula.

Specimens of *E. mastersi* differ more substantially in: pattern of setae on integument,

the presence of abdominal sclerites, lack of prolegs, the number of mandibular teeth, and the smaller and more distal lateral protuberance on the second antennal segment. The species is separately described below.

Identification

By rearing larvae collected in the field.

Remarks

The larvae of the Australian *E. (Methydus) maculiceps* (MacLeay) (Anderson 1976) and *E. (M.) eyrensis* differ little from those of the North American *E. (Lumetus) ochraceus* (Melsheimer) (Archangelsky 1997) and *E. (L.) fimbriatus* (Richmond 1920, as *E. perplexus* (le Conte)) except possibly in a squatter mentum. *Enochrus (Hydatotrepis) mastersi* differs from all of the above by the nearly symmetrical mandibles and the lack of obvious setiferous prolegs, and from *E. (M.) eyrensis*, by the more elongate and spinose mentum. In these characters, other than the absence of prolegs, it more closely resembles larvae of the subgenus *Lumetus* than those of *Methydus*.

All known larvae of *Enochrus* share with most *Helochaeres* the angled nasale. Apart from *E. mastersi*, they are readily separated from *Helochaeres* by the asymmetrical mandibles. *Enochrus mastersi* can be separated from *Helochaeres* by having the ligula shorter rather than longer than the basal segment of the labial palpus, in the lack of a basal patch of strong setae on the maxillary stipe, and in the presence of small dorsal sclerites on the abdominal segments.

Specimens examined

South Australia: 2 km S Penola, 10/99.

Enochrus sp. **Queensland:** Bohle River, 10 km N Townsville, 23/3/96; 30 km SE Townsville 4/5/98. **South Australia:** Mandina Lakes, 15/10/00; Tea Tree Gully, 7/5/97.

Enochrus mastersi (W. MacLeay). Fig. 7

Size of third instar. Length 12.0 mm; head capsule 1.30 mm long, 1.13 mm wide.

Head capsule. Subquadrate. Labroclypeus weakly asymmetrical; nasale obliquely truncate, left side shorter than right, with seven to eight short teeth, first two on right side and last one on left side largest; left lobe of epistome more rounded than right, shorter than nasale. Frontal sulci as an inverted bell, fusing before reaching occipital foramen. Coronal sulcus very short.

Gular sclerite absent. Cervical sclerites small, subrectangular.

Antennae. Three-segmented. First segment wider than second segment, shorter than second in first instar larvae, about 1.5 times as long as second in third instar larvae, slightly bulging on inner apical corner; third segment about a third the length of the second. Sensory appendage on second segment much shorter than third segment.

Mandibles. Weakly asymmetrical; right mandible with two strong inner teeth on basal half; left mandible with one strong inner tooth and one much weaker tooth. Inner margins of distal teeth and distal parts of mandibles serrated.

Maxillae. Five-segmented. Stipes wide, much longer than remaining segments combined, with four strong setae on inner margin. Palpus four-segmented; first segment subrectangular, as wide as long, with an inner process a little shorter than second palpal segment; second segment short; third and four segments slightly longer, subequal in length.

Labium. Mentum rectangular, dorsal surface with scattered cuticular spines and several strong spines at front and side edges. Prementum rounded, a little wider at base, shorter than mentum. Palpus two-segmented, first segment short, second segment 1.0–1.5 times longer than first, some small spines at the bases of both segments. Ligula slender, as long as first palpal segment.

Thorax and legs. Prothorax completely covered by a dorsal sclerite, with sagittal line, with numerous relatively long setae; ventral surface with two subrectangular sclerites. Mesothorax with a pair of large dorsal sclerites with irregular posterior margins, covered with relatively long setae. Metathorax with narrow pair of dorsal sclerites each with a small foot-shaped backward extension, covered with relatively long setae. Legs five-segmented, well developed, visible in dorsal view.

Abdomen. Segments 1 to 7 similar in shape and size, subdivided into three or four transverse folds; segments 1 to 6 with a dorsal pair of small suboval sclerites. Segment 8 with a large, suboval, dorsal sclerite. Segment 9 trilobed, with a pair of short one-segmented urogomphi. Integument covered with dense, small setae, in many places organised into tight bundles.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

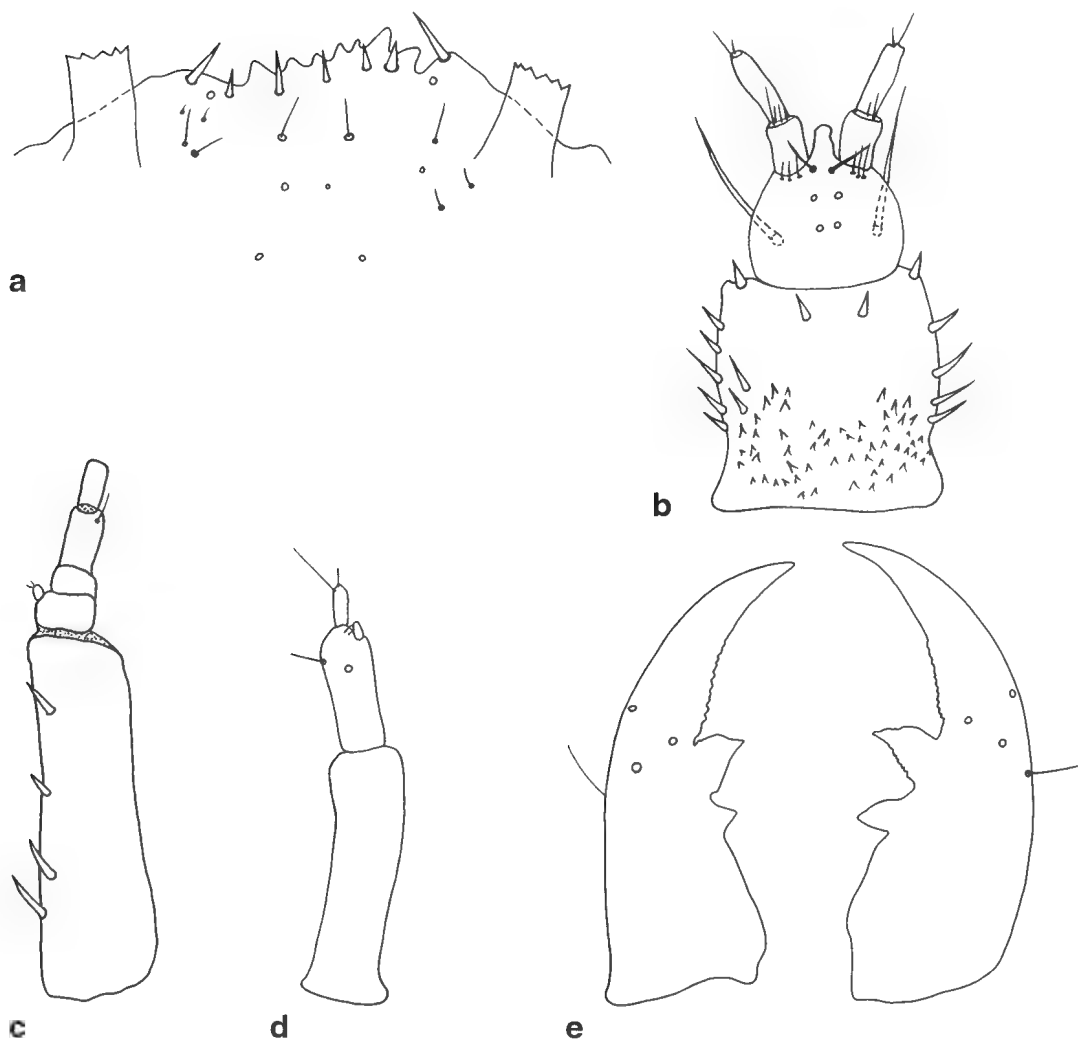


FIGURE 7. *Enochrus mastersi*. a, labroclypeus; b, labium; c, maxilla; d, antenna; e, mandibles.

Intraspecific variation

Only three specimens are known. They vary slightly in size of the abdominal sclerites but otherwise are very similar.

Interspecific variation

See under *E. eyrensis*.

Identification

By association and elimination.

Specimens examined

New South Wales: Salisbury, 26/11/95.

Northern Territory: Ormiston Gorge, 27/1/99.

Victoria: King Parrot Creek, 2/12/98.

Helochaeres Mulsant

Helochaeres tristis W. MacLeay. Fig. 8

Size of third instar. Length 6.8–10.0 mm; head capsule, 0.53–0.56 mm long, 0.66–0.69 mm wide.

Head capsule. Subquadrate. Labroclypeus asymmetrical; nasale obliquely truncate, shorter on left side, with six small teeth; lateral lobes of epistome project nearly as far as nasale. Frontal sulci inversely bell-shaped, meeting before reaching occipital foramen. Coronal sulcus very short. Gular sclerite absent. Cervical sclerites narrow, subrectangular.

Antennae. Three-segmented. First segment as

long as second (first instar larvae) or longer (second and third instar larvae); second segment with a slim apical sensory appendage on inside which is half the length of third segment; third segment much smaller than second.

Mandibles. Slightly asymmetrical; two inner teeth in middle, distal one larger on left mandible, only slightly larger on right mandible. Distal inner margin and inner margins of teeth slightly serrated. Distal part of teeth darker.

Maxillae. Five-segmented. Stipes wide, longer than remaining segments combined, with a row of four stout setae on inner margin, base with a tuft of strong spines. Palpus four-segmented; first segment subrectangular, with an inner process a little longer than the second palpal segment; second segment the shortest; third segment longest; last segment slightly shorter than third.

Labium. Mentum large, subquadrate, with dorsal surface covered by strong cuticular spines. Prementum subrectangular, wider than long. Palpus two-segmented, basal segment very short, distal segment three to four times longer than basal; a few small spines at base of apical segment. Ligula about twice as long as first palpal segment.

Thorax and legs. Prothorax almost completely covered by a dorsal sclerite, with sagittal line; ventral surface with a subrectangular plate, with a sagittal line. Mesothorax with a pair of large rectangular dorsal sclerites; metathorax with a pair of small dorsal sclerites, irregular in shape, composed of a wide and narrow basal portion and an L-shaped central portion arising from the middle of the basal piece. Legs five-segmented, well developed, visible in dorsal view.

Abdomen. Segment 1 with two dorsal pairs of small, narrow, irregularly shaped sclerites; anterior pair much smaller. Segments 1 to 7 similar in size and shape, subdivided by three or four transverse folds; pleura of segments 1 to 7 with three longitudinal slight bulges, the most ventral one in three lobes, each segment with a dorsal pair of setae towards the middle arising from a small circular sclerite or dark-pigmented area, and a small seta a little inwards and backwards from each spiracle. Segment 8 with a large, suboval, dorsal sclerite, serrate on posterior edge and pair of short apical flaps. Segment 9 trilobed; with a pair of small one-segmented urogomphi; central lobe largest. Integument densely covered in short fine setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal, raised slightly above the surface. Mesothoracic and first seven abdominal spiracles

non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

There is some variation in the shape of the thoracic sclerites and in the shape and configuration of the nasale teeth.

Interspecific variation

H. luridus (W. MacLeay) and *H. clypeatus* Watts. As for *H. tristis*.

H. tenuistriatus Regimbart. The integument is predominantly covered by long thin setae rather than the short and very curved setae found in *H. tristis*, *H. luridus* and *H. clypeatus*. This gives a distinct furry look to the larvae.

H. foveicollis (Montrouzier). Differs in lacking nasale, having a slight bulge on the inside of antenna and a number of other characters (see below). These differences are sufficient to warrant a separate description (see below).

Other *Helochares* species. Within specimens unidentified to species there is variation in: form of the small setae on the integument; the shape of the metasternal sclerites; and the presence/absence, position and shape of the abdominal sclerites.

Identification

H. tristis, *H. luridus* and *H. clypeatus* by rearing larvae collected in the field; *H. tenuistriatus* by association and elimination.

Remarks

Within the known Australian *Helochares* larvae there are clearly two groups: *H. foveicollis*; and *H. tristis*, *H. luridus*, *H. tenuistriatus* and *H. clypeatus*. These correspond to the subgenera *Helochares* and *Hydrobaticus* Blackburn, respectively, and strongly reinforce the distinctiveness of these groups as reflected in the classification. Within Australian *H. (Hydrobaticus)* there is very little difference between the known species or among the large number of unidentified larvae. In addition, there is minimal difference between these Australian *H. (Hydrobaticus)* and the North American *H. (Hydrobaticus) maculicollis* Mulsant (Archangelsky 1997; Richmond 1920) or the South American *H. (Sindolus) talarum* Fernandez and *H. (Helochares) pallipes* (Brulle) (Fernandez 1983) or the European *H. (Helochares) obscurus* (Muller) (as *griseus* Heer) (Boving & Henriksen 1938).

The larvae of *H. (Helochares) foveicollis* differ

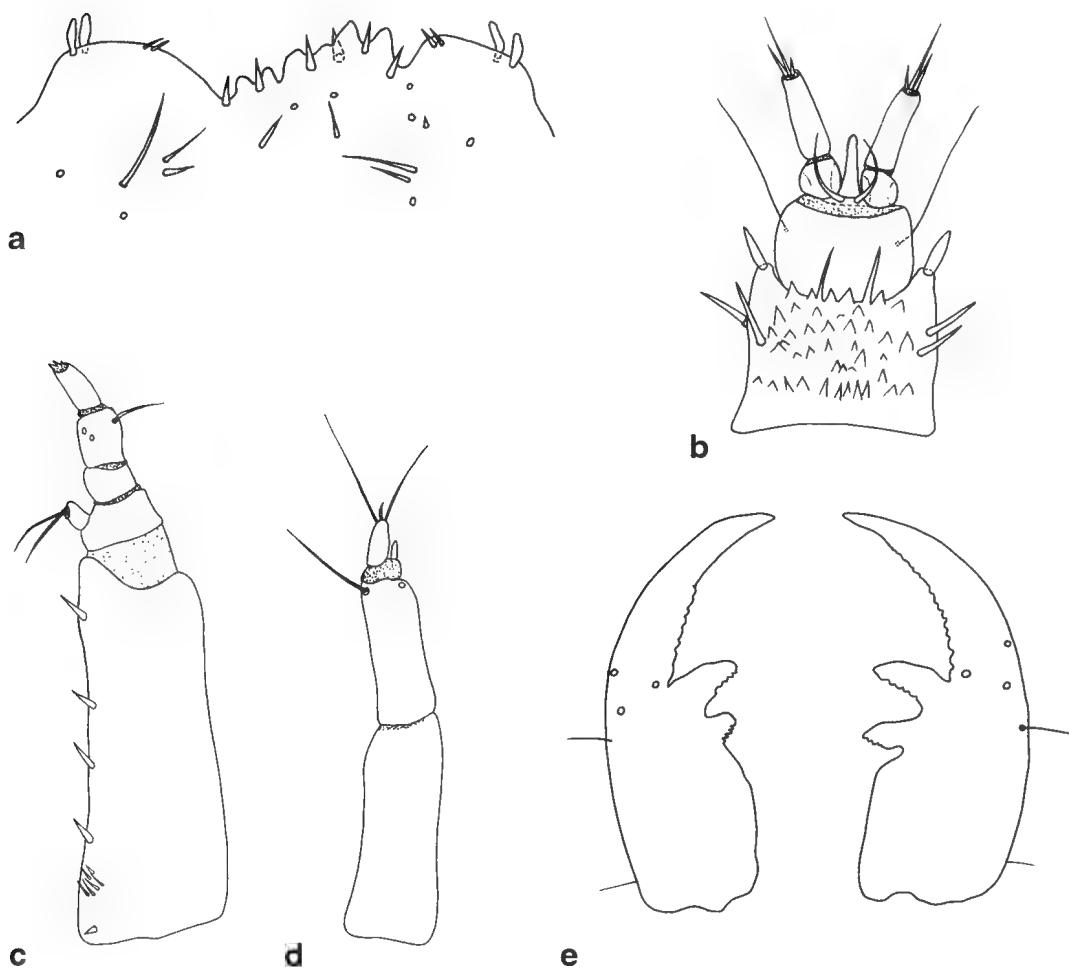


FIGURE 8. *Helochaeres tristis*. a, labroclypeus; b, labium; c, maxilla; d, antenna e, mandibles.

considerably from all of these species in a number of characters, most noticeably the symmetrical labroclypeus and the more elongate antennae and maxillary palpi (see later).

The larva of the related Australian genus, *Chasmogenus*, is only known from the work of Anderson (1976). It also has a symmetric labroclypeus but differs from both *H. (Helochaeres) foveicollis* and *H. (Hydrobaticus) tristis* in the asymmetric mandibles, one with one tooth and the other with two, and in the complete rather than partial dorsal sclerites on the metathorax.

Species of *H. (Hydrobaticus)* appear to breed more or less continuously and females are frequently caught with egg masses attached to

their abdomens, although Anderson (1976) found that there was a distinct spring breeding season in *H. tristis* near Sydney. Larvae are among the most commonly collected Hydrophilid larvae, often found together with those of *Limnoxenus* in the south and both *Limnoxenus* and *Sternolophus* in the north. They can be readily separated from both of these by their angled nasale and mandibles with two rather than three teeth.

Although adults of *Enochrus* are often more common than those of *Helochaeres*, their larvae are, for unknown reasons, rarely found. They share with *H. (Hydatotrephis)* the angled nasale but, other than *E. mastersi*, have strongly asymmetrical mandibles. Larvae of *E. mastersi* resemble those of *H. (Hydatotrephis)* quite closely

but differ in lacking a cluster of strong setae at the base of the maxillary palpus, and in having the ligula shorter than the basal segment of the labial palpus.

Specimens examined

New South Wales: 20 km W Nelligan, 3/11/97. **South Australia:** 10 km N Coonawarra, 26/9/98; Cudlee Creek, 10/11/96; Kuitpo, 5/10/95; 13 km W Meadows, 26/9/96; Mt Crawford State Forest, 10/11/96; Tea Tree Gully, 7/5/97. **Victoria:** 10 km W Cowwarr, 30/11/98; Healsville, 12/68.

H. tenuistriatus. **Western Australia:** 30 km N Perth, 14/10/96

H. clypeatus. **Northern Territory:** Nourlangie Creek, 20 km SSW Jabiru, 11/10/98.

H. luridus. **Queensland:** Burdekin River E of Charters Towers, 4/5/98.

Helocharus sp. **New South Wales:** 12 km E Tamworth, 26/11/95. **Northern Territory:** Nawurlandja, Kakadu National Park, 22/3/98. **Queensland:** Alligator River 20 km S Townsville, 25/3/96; Bluewater, 22/3/96; Bowling Green Bay National Park, 6/11/95; 10 km N Cairns, 4/1/97; Eubenangee Swamp, 4/2/97; 8 km S Greenvale, 27/3/96; Jourama Falls near Townsville, 31/10/95; 1 km W Mingela, 4/5/98; Star River, 1/11/95; 30 km SE Townsville, 4/5/98.

Helochares foveicollis (Montrouzier). Fig. 9

Size of third instar. Length 13.5 mm; head capsule 0.78 mm long, 0.94 mm wide.

Head capsule. Subquadrate. Labroclypeus symmetrical, without nasale; with eight to nine small teeth along front edge in middle; lateral lobes of epistome slight. Frontal sulci inversely bell-shaped, meeting before reaching occipital foramen. Coronal sulcus short. Gular sclerite absent. Cervical sclerites small, subrectangular.

Antennae. Three-segmented. First segment as long as second (first instar larvae) or longer (second and third instar larvae), with distinct protruberance on inside near apex; second segment with a slim apical sensory appendage on inside, half the length of third segment; third segment much thinner than second.

Mandibles. Relatively slim, symmetrical; two inner teeth in middle, distal one much larger. Outer margin of apical tooth weakly serrated.

Maxillae. Five-segmented. Stipes relatively narrow, much longer than remaining segments combined, with a row of five stout setae on inner

margin, base with a few short, strong spines. Palpus four-segmented; first segment subrectangular with an inner process as long as the second palpal segment; second segment the shortest; third segment the longest; fourth segment shorter than third.

Labium. Mentum large, subquadrate, with central portion of dorsal surface covered by weak cuticular spines and a semicircle of six spines, anterolateral angles sharp, each with a small spine. Prementum elongate-rectangular, longer than wide. Palpus two-segmented, basal very short, distal segment four to five times longer than basal one. Ligula short, thick, about twice the length of first palpal segment.

Thorax and legs. Prothorax almost completely covered by a dorsal sclerite, with sagittal line; ventral surface with a subrectangular sclerite, subdivided by a sagittal line. Mesothorax with a pair of large dorsal sclerites; metathorax with a pair of small dorsal sclerites composed of a wide and narrow basal portion and an L-shaped portion arising from the middle of the basal piece, 'heel' reaching posterior margin. Legs five-segmented, well developed, visible in dorsal view.

Abdomen. Segments 1 to 7 similar in size and shape, subdivided by three or four transverse folds; segment 1 with two dorsal pairs of small narrow basal sclerites, the anterior pair smallest; pleura of segments 1 to 7 each with three to four weak longitudinal bulges, a well separated pair of strong dorsal setae arising from a very small circular darkly pigmented area, a moderately strong seta just inwards and behind each spiracle. Segment 8 with a large, suboval, dorsal sclerite with a ragged hind edge, and a pair of prominent apical flaps; segment 9 trilobed, central lobe largest and sclerotised, with a pair of prominent one-segmented urogomphi. Integument covered with moderately dense hair-like setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles very small, non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

Among the few specimens known there is some variation in the number of larger spines on the mentum and in wear on the nasale teeth.

Interspecific variation

Helochares foveicollis differs from other known Australian *Helochares* larvae by the lack of a nasale, presence of a prominent bulge on the

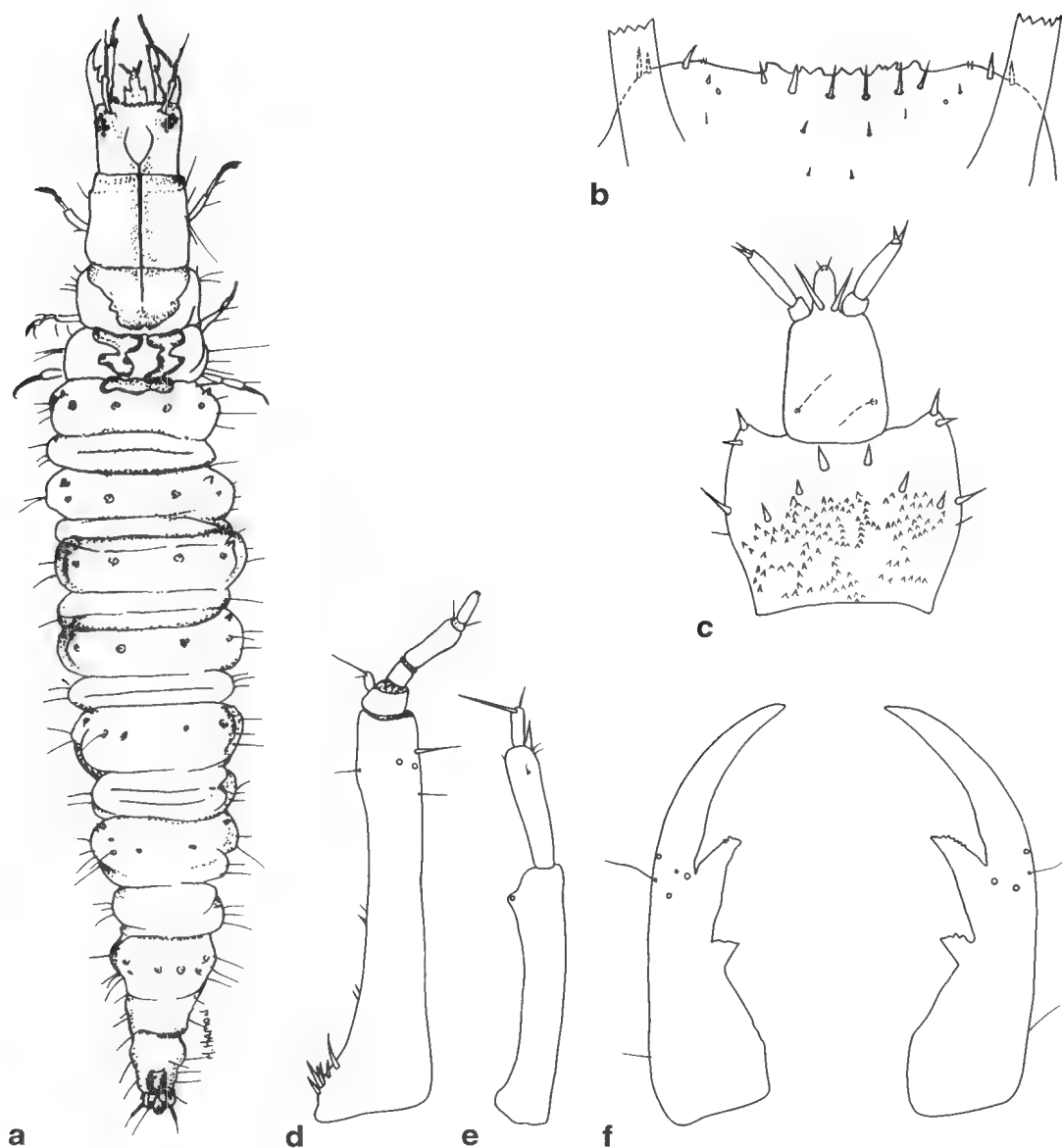


FIGURE 9. *Helochaeres foveicollis*. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandibles.

inside of the antennae, proportionally longer and narrower prementum and ligula, more elongate maxillary palpi and the shape of the metathoracic sclerites (Fig. 9).

Identification

By rearing field-caught larvae and rearing from egg mass attached to female.

Remarks

On adult characters *H. foveicollis* is presently placed in the subgenus *Helochaeres* together with *H. obscurus* and *H. pallipes*. However larval characters do not support this placement, nor its placement in either of the subgenera *Hydatotrephis* or *Sindolus*.

Specimens examined

Northern Territory: Manton Dam, 2/2/99; 2 km S Adelaide River, 1/2/99. **Queensland:** 40 km S Townsville, 2/2/97.

Hybograllius Orchymont

Hybograllius hartmeyer (Regimbart). Figs 10, 17b

Size of third instar. Length 10.0 mm; head capsule 1.60–1.79 mm long, 1.62–2.00 mm wide

Head capsule. Rectangular. Labroclypeus asymmetrical; nasale narrow, projecting well forward, with five teeth, the two lateral ones more distant than rest; lateral lobes of epistome rounded, projecting farther than nasale, left lobe often larger, with a strong comb of stout spines on front edge, front edge of right lobe with a few scattered spines. Frontal sulci U to V-shaped, fusing just before reaching occipital foramen. Coronal sulcus short. Gular sclerite absent. Cervical sclerites relatively small, subrectangular.

Antennae. Three-segmented. First segment longer than remaining segments combined; second segment about 1.5 times the length of third segment which is very thin. Sensory appendage on second segment minute.

Mandibles. Asymmetrical; right mandible with three inner teeth, the anterior one largest; left mandible with three teeth of approximately the same size, central one with patch of strong setae at base.

Maxillae. Five-segmented. Stipes stout, longer than remaining segments combined, with four long stout setae on inner margin. Palpus four-segmented; first segment widest, with a short inner process; second segment short; third segment longest; fourth segment about half length of third.

Labium. Mentum small, subrectangular, sides slightly convex, dorsal surface with small spines, anterolateral angles rounded with several stout spines. Prementum elongate, rectangular, as long as mentum. Palpus two-segmented, first segment the shortest. Ligula present, about as long as the first palpal segment, tip weakly bifid.

Thorax and legs. Prothorax with large dorsal sclerite, with sagittal line; ventral surface with a large subrectangular sclerite, with sagittal line. Mesothorax with a pair of large triangular dorsal sclerites. Metathorax with a pair of semicircular dorsal sclerites and a more posterior pair of much smaller circular ones. Sclerites, particularly the

anterior ones, covered with very short spines, occasionally arranged in short rows; rest of thorax densely covered with short fine setae with a few much longer setae laterally. Legs five-segmented, relatively short, just visible in dorsal view.

Abdomen. Segments 1 to 8 similar in shape, tapering towards the caudal end; Segments 1 to 7 subdivided into three or four transverse folds; sides of each segment with some slight, fleshy bulges, with one to two long setae. Segment 8 with two transverse folds, without dorsal sclerite. Segment 9 with hind margin weakly concave. Below segment 9, and projecting just beyond, are two prominent broad lobes. Integument densely covered with small fine setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles on small papillae. Spiracles on segment 8 (if present at all) obsolete and certainly non-functional.

Pupa (Fig. 17b). Head without styli. Pronotum with 22 styli, 16 around margins and 6 on disc. Mesonotum and metanotum each with one pair of styli near the midline. Abdominal segments 1 to 7 with a row of four styli on the terga, segments 2 to 7 with one stylus on each pleuron; segment 8 without styli; segment 9 with a pair of long urogomphi.

Intraspecific variation

One specimen has a slight mandibular tooth anterior to the normal ones (Fig. 1); otherwise, there is little variation other than in tooth wear between the few known specimens.

Identification

By rearing from larvae collected in the field.

Specimens examined

Western Australia: Gooseberry Hill, 14/9/00.

Remarks

Hybograllius is a monospecific Australian genus known only from a couple of localities in the escarpment region of the Darling Ranges east of Perth, Western Australia where it lives in small temporary winter/spring streams. Although placed with *Limnoxenus* in the subtribe Hydrobiina of the tribe Hydrophilini (Hansen 1991), the larvae of the two genera have little in common. Several features of the larvae of *Hybograllius* stand out: the lack of a spiracular atrium, the strongly asymmetric labroclypeus, the narrow prominent nasale, the strongly asymmetrical mandibles, and the rings of small spines at the base of the

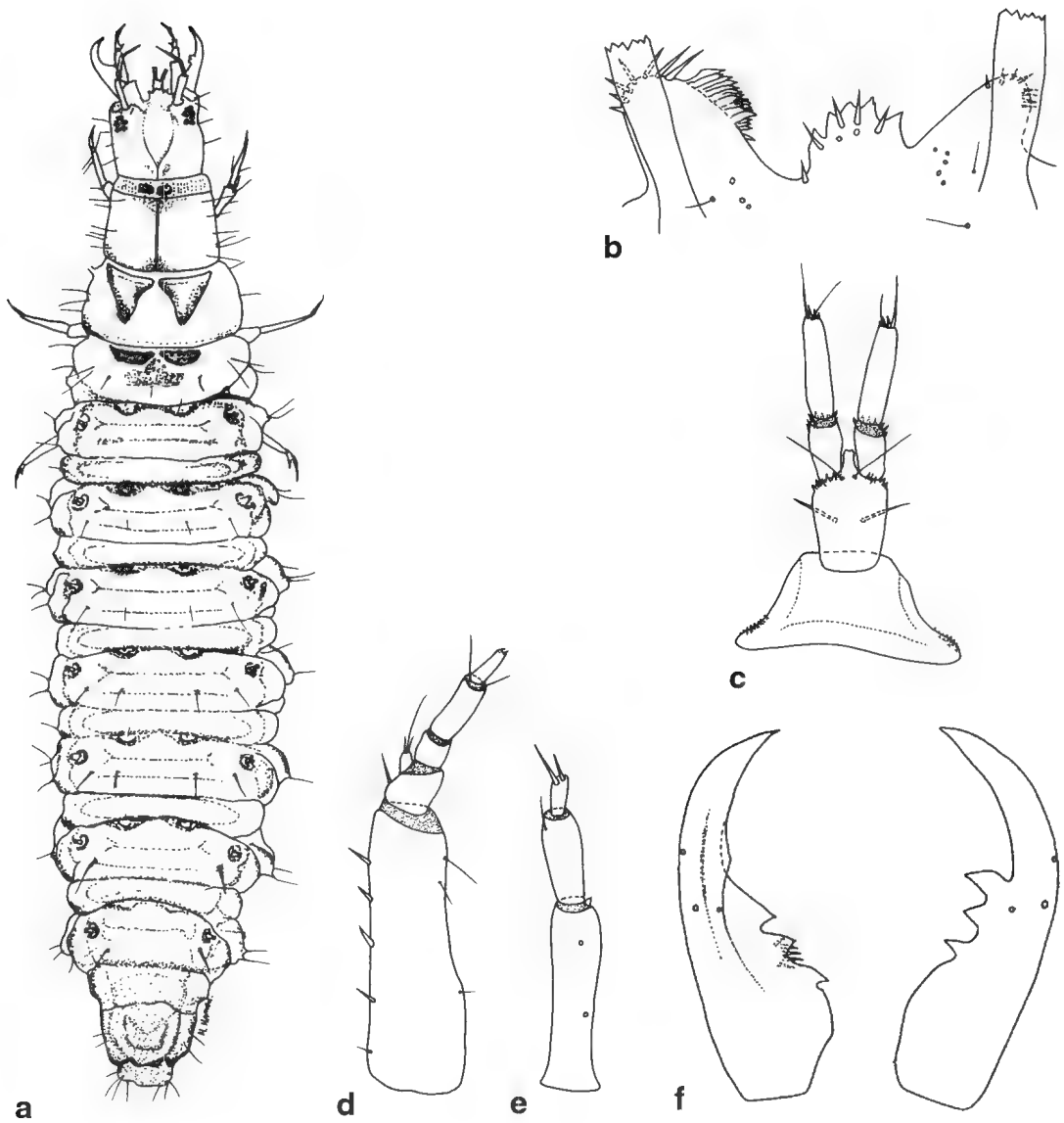


FIGURE 10. *Hybograllus hartmeyeri* a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandibles.

segments of the labial palpi. In most of these characters it most closely resembles *Berosus*. Apart from the lack of a spiracular atrium and the presence of a coronal sulcus, it also resembles the larvae of *Oocyclus* Sharp and *Laccobius* in the tribe Laccobiini. To what degree these similarities reflect phylogenetic relationships remains to be seen.

As well as the lack of a functional apical spiracle, the main tracheal trunks are narrower than most other genera and the spiracles are not

much larger, if at all, than those of other genera where they are considered non-functional. How the larvae manage to breathe is a puzzle.

Hydrobiomorpha Blackburn

Hydrobiomorpha sp. Fig. 11

Size of third instar. Length 15.0 mm; head capsule 1.65 mm long, 1.70 mm wide.

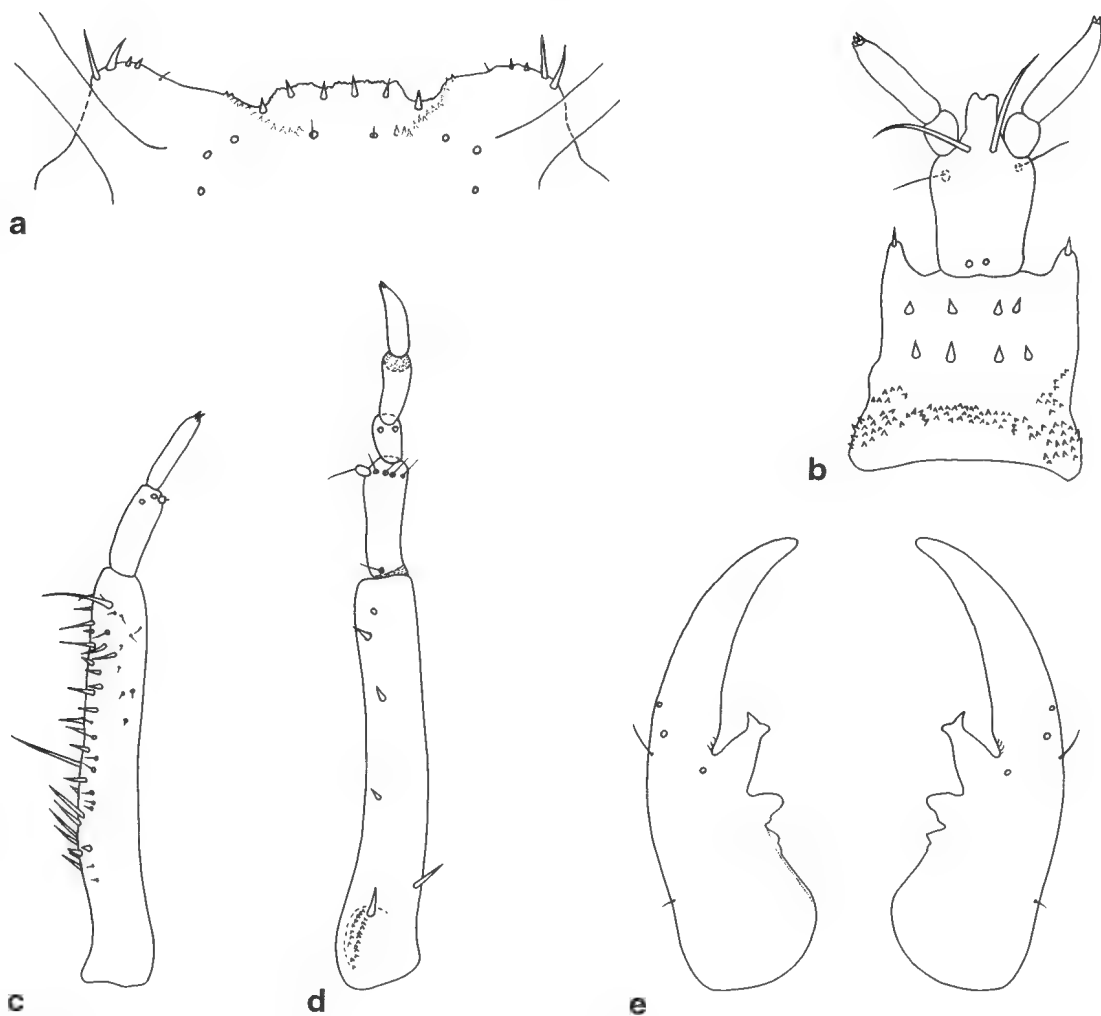


FIGURE 11. *Hydrobiomorpha* sp. **a**, labroclypeus; **b**, labium; **c**, maxilla; **d**, antenna; **e**, mandibles.

Head capsule. Subquadrate. Labroclypeus slightly asymmetrical; nasale truncate, edge rough rather than toothed; lateral lobes of epistome rounded, projecting further than nasale. Frontal sulci V-shaped, meeting before reaching occipital foramen. Coronal sulcus short. Gular sclerite absent. Cervical sclerites small, subquadrate. Numerous small darker patches on posterolateral angles and within frontal sulci.

Antennae. Three-segmented. First segment slender, three times longer than remaining segments combined (third instar larvae), inner margins with numerous short spines; second segment as long as third. Sensory appendage of second segment very small.

Mandibles. Symmetrical, sharply pointed; right mandible with three teeth on basal half, distal one large, bifid apically, central tooth smaller, basal one much smaller; left mandible similar to right except for basal tooth placed slightly more ventrally.

Maxillae. Five-segmented. Stipes slender, longer than remaining segments combined, with a group of short spines on inner margin at base, and several setae along inner and outer margins. Palpus four-segmented; first segment longest, with a short inner process; second segment the shortest; third and fourth segments subequal in length, each twice as long as second segment.

Labium. Mentum approximately square,

anterolateral angles projected, each with a pair of very small spines; dorsal surface with eight short, stout setae on distal two-thirds, and short cuticular spines on basal third. Prementum longer than wide, half the width of mentum. Palpus two-segmented, distal segment three to four times longer than basal segment. Ligula a little longer than first palpal segment, weakly bifid.

Thorax and legs. Prothorax covered by a large dorsal sclerite, posterior end rounded, sagittal line present; ventral sclerite large, subrectangular, with sagittal line. Mesothorax with pair of irregularly shaped sclerites, wider anteriorly, with sagittal line. Metathorax with pair of small irregular shaped sclerites. Legs five-segmented, long, visible in dorsal view. Prothorax and mesothorax covered with small, scattered, dark patches.

Abdomen. First segment subdivided into two transverse folds, with a dorsal pair of narrow sclerites near anterior edge; segments 2 to 7 subdivided into four or five transverse folds, without sclerites. Segments 1 to 7 each with eight setose tubercles, four dorsal and two on each lateral margin; pleura weakly lobed. Segment 8 with a small, suboval, dorsal sclerite, posterior apex subdivided into four lobes and a pair of small procerci. Segment 9 round, with three small dorsal sclerites, bearing a pair of short, one-segmented urogomphi, and a pair of long paracerci; a pair of gill-like appendages (prostyli) originate on ventral side. Integument sparsely covered with relatively long setae. Single, narrow, darker line along midline of dorsal surface.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Identification

Agreement with generic description by Archangelsky (1997). Specimens were taken in association with *H. bovilli* Blackburn and are almost certainly that species.

Interspecific variation

There is little variation between the two known specimens.

Remarks

The larvae described above differ little from those of the New World *H. casta* (Archangelsky 1997; Spangler 1973) or the unidentified African species described by Berge Henegouwen (1982).

The peculiar shape of the anterior mandibular tooth is diagnostic within the Australian fauna.

Specimens examined

Northern Territory: Holmes Jungle, 28/11/99.

Hydrophilus Geoffroy

Hydrophilus bilineatus (MacLeay). Fig. 12

Size of third instar. Length 35 mm; head capsule 3.25 mm long, 4.25 mm wide.

Head capsule. Suboval. Labroclypeus virtually symmetrical; nasale undeveloped; lateral lobes of epistome rounded, projecting farther than nasale. Frontal sulci broadly U-shaped, fusing just before reaching occipital foramen. Coronal sulcus present, very short. Gular sclerite absent. Cervical sclerites small, suboval.

Antennae. Four-segmented. First segment slender, slightly constricted near base, longer than remaining segments combined, with some slender setae on distal two-thirds of inner margin; second segment short, constricted near base in first instar larvae, third and fourth segments subequal in length. Sensory appendage on third segment reduced to a small papilla.

Mandibles. Asymmetrical; right mandible longer, more slender, with a large tooth on basal half which is divided by a longitudinal groove into ventral and dorsal sections; left mandible shorter, with one small inner tooth on basal half.

Maxillae. Five-segmented. Stipes narrow, elongate, longer than remaining segments combined, with three stout setae on inner margin. Palpus four-segmented; first segment the longest, with a short inner process; second and third segments subequal in length; fourth segment slightly shorter.

Labium. Mentum subrectangular, sides convex, anterolateral angles lobed, central third with some small spines (without spines in first and second instars). Prementum subtrapezoidal, anterior end wider with a pair of small protuberances towards front. Palpus two-segmented, first segment shortest. Ligula present, much shorter than first palpal segment.

Thorax and legs. Prothorax with two large sclerites together covering most of dorsal surface, the triangular area anterior to these sclerites usually sclerotised; ventral surface with a large subrectangular sclerite, with sagittal line. Mesothorax with a pair of subtriangular dorsal sclerites. Metathorax with a pair of narrow, basal

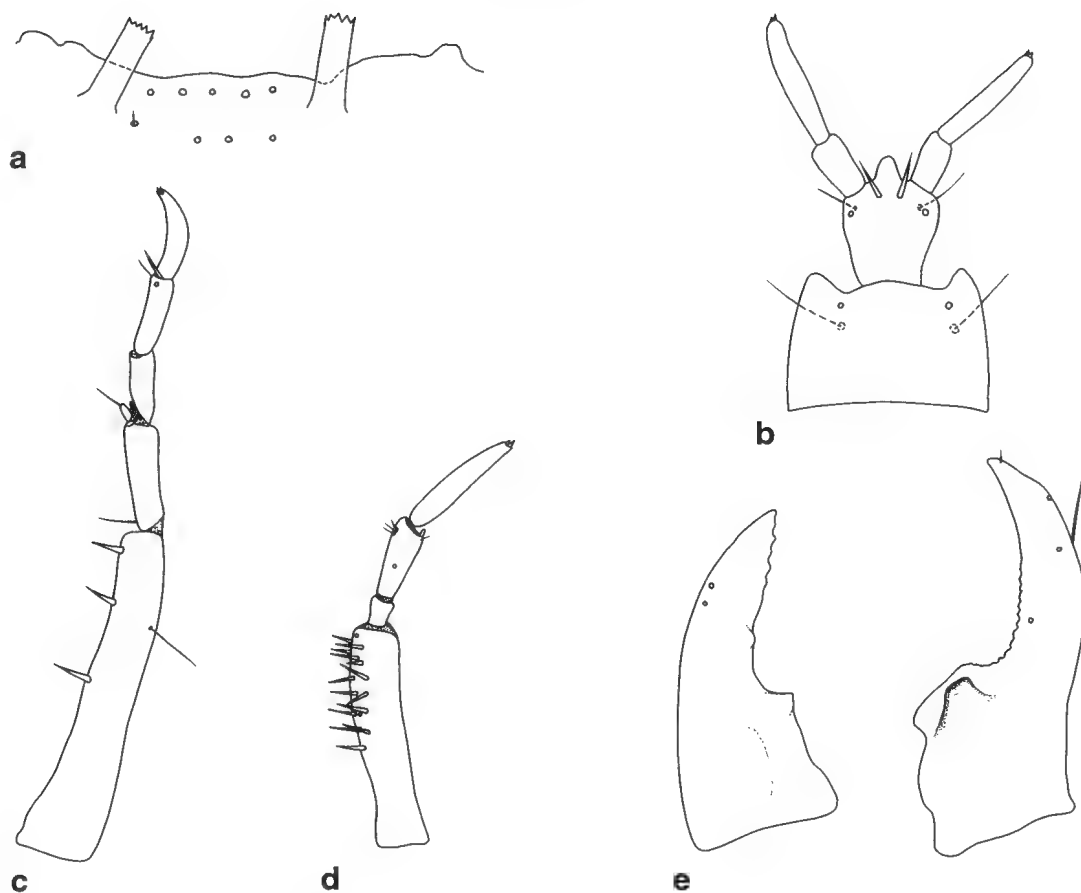


FIGURE 12. *Hydrophilus bilineatus*. a, labroclypeus; b, labium; c, maxilla; d, antenna; e, mandibles.

sclerites and a more central pair of small irregularly-shaped ones. Legs five-segmented, relatively short, visible in dorsal view, with rows of long swimming setae on both dorsal and ventral edges of femur and tibiotarsus.

Abdomen. Segments 1 to 6 similar in shape, tapering towards the caudal end; segments 7 to 8 more elongate and slender. Segments 1 to 7 subdivided into three transverse folds; third fold with two lateral and two dorsal small tubercles, more obvious on posterior segments. Pleura 1 to 8 each with a small lateral tubercle. Segment 8 with two small subtriangular sclerites at posterior end; segment 9 slightly trilobed, with a pair of short one-segmented urogomphi, ventromedially with a pair of long gill-like appendages. Integument in first instar very densely covered with small thin setae; in second and third instars moderately

covered with thin, relatively long setae and numerous small 'bumps'.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles very small, non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Identification

By association and elimination.

Intraspecific variation

I have not noticed any significant variation within the few available specimens I have identified as *H. bilineatus*.

Interspecific variation

Within the larvae available there is considerable

variation in a number of characters, most notably: number of antennal segments vary from three to four; the presence/absence/form of the lateral projections on the abdominal segments; form of covering of the integument; dorsal colour pattern.

Remarks

The larvae of two European species, *H. piceus* Linnaeus and *H. aterrimus* Eschscholtz, and the North American *H. triangularis* (Say) are well known (Archangelsky 1997; Boving & Henriksen 1938; Richmond 1920). In addition, the larvae of *H. senegalensis* (Percheron) (Berge Henegouwen 1982; Africa) and *H. acuminatus* Motschulsky (Morioka 1955; Japan) have been described. Within the known larvae there is considerable variation in the number of antennal segments in different instars, in the development of lateral abdominal flaps and, at least within the Australian species, in the form of the integument coverage. Somewhat unusually for Hydrophilidae larvae, it appears that specific differences are sufficient to enable the larvae of many species to be identified.

In the lack of lateral abdominal flaps and its four segmented antennae, *H. bilineatus* most closely resembles the North American *H. triangularis* but differs in a number of details, most obviously in the more robust mandibles with a well-developed molar region. The other Australian species appear more distant, particularly in the well-developed abdominal flaps and number of antennal segments. With the more robust mandibles and abdominal flaps these Australian species appear to be closer to the subgenus *Diblocelus* (sensu Hansen 1991) than subgenus *Hydrophilus* (Archangelsky 1997). On adult characters they fit clearly into the subgenus *Hydrophilus*.

Egg cases of several species were collected in the field and each produced between 15 and 30 larvae. Those thought to be of *H. bilineatus* refused all food offered but the other species accepted, often with some excitement, small snails and some accepted freshly killed mosquito larvae. None accepted chironomid larvae. Unfortunately, despite seemingly accepting snails as food, none was reared to the second instar. Species varied in the degree of cannibalism. Some broods were quite strongly cannibalistic but in others, apart from the occasional unfortunate individual, siblings lived well together.

Specimens of *Hydrophilus bilineatus* (MacLeay) have previously been identified as *H. picicornis* Chevrolat (Hansen 1999).

Specimens examined

Northern Territory: Manton Dam, 23/3/97; 2 km S Adelaide River 1/2/99.

Hydrophilus sp. **Northern Territory:** Newry Station, 2/86 col. M. J. Tyler. **Queensland:** 25 km S Townsville, 3/5/98, 2/2/97; 8 km S Greenvale, 27/3/96; 5 km NE Mt Molloy, 30/3/96. **South Australia:** 10 km N Coonawarra, 10/11/97, 16/10/97; 1 km S Nangwarra, 9/10/97. **Tasmania:** 12 km N Hobart, 2/12/00; 2 km W Fingle, 23/1/00; 3 km SW Clifton Beach, 4/12/00. **Victoria:** 5 km NE Dartmoor, 11/10/97. **Western Australia:** Murchison River, 13/3/95, col. S. Halse; 6 km S Pinjarrah, 23/10/96.

Laccobius Erichson

Laccobius decipiens Gentili. Fig. 13

Size of third instar. Length 5.0–6.5 mm; head capsule 0.43–0.50 mm long, 0.45–0.46 mm wide.

Head capsule. Subrectangular. Labroclypeus strongly asymmetrical; nasale prominent, with three teeth; lateral lobes of epistome asymmetrical, both projecting further than nasale; left lobe larger, covering basal third of mandible, with a row of about 12 strong curved setae on inner margin, larger ones dentate; right lobe smaller, covering a quarter of mandible, without setae. Frontal sulci parallel, reaching occipital foramen without coming together, difficult to see in third instar larvae. Coronal sulcus absent. Gular sclerite absent; cervical sclerites small and oval, difficult to see in first instar larva.

Antenna. Three-segmented; second segment the longest, with a small outer sensory appendage about a quarter the length of third segment; first segment half the length (first instar larvae) to slightly shorter (third instar larvae) than second segment.

Mandibles. Strongly asymmetrical. Left mandible with three inner teeth, central one largest, with five strong spines, region behind third tooth with a number of very short spines; right mandible with two inner teeth, larger than those of left mandible, front one much larger, occasionally also with a very small third tooth, or spine, behind the second.

Maxillae. Five-segmented. Stipes wide, longer than remaining segments combined, inner margin with four setae. Palpus four-segmented; first segment subquadrate, incompletely sclerotised, with a small inner process; second segment shortest; third and fourth segments subequal in length.

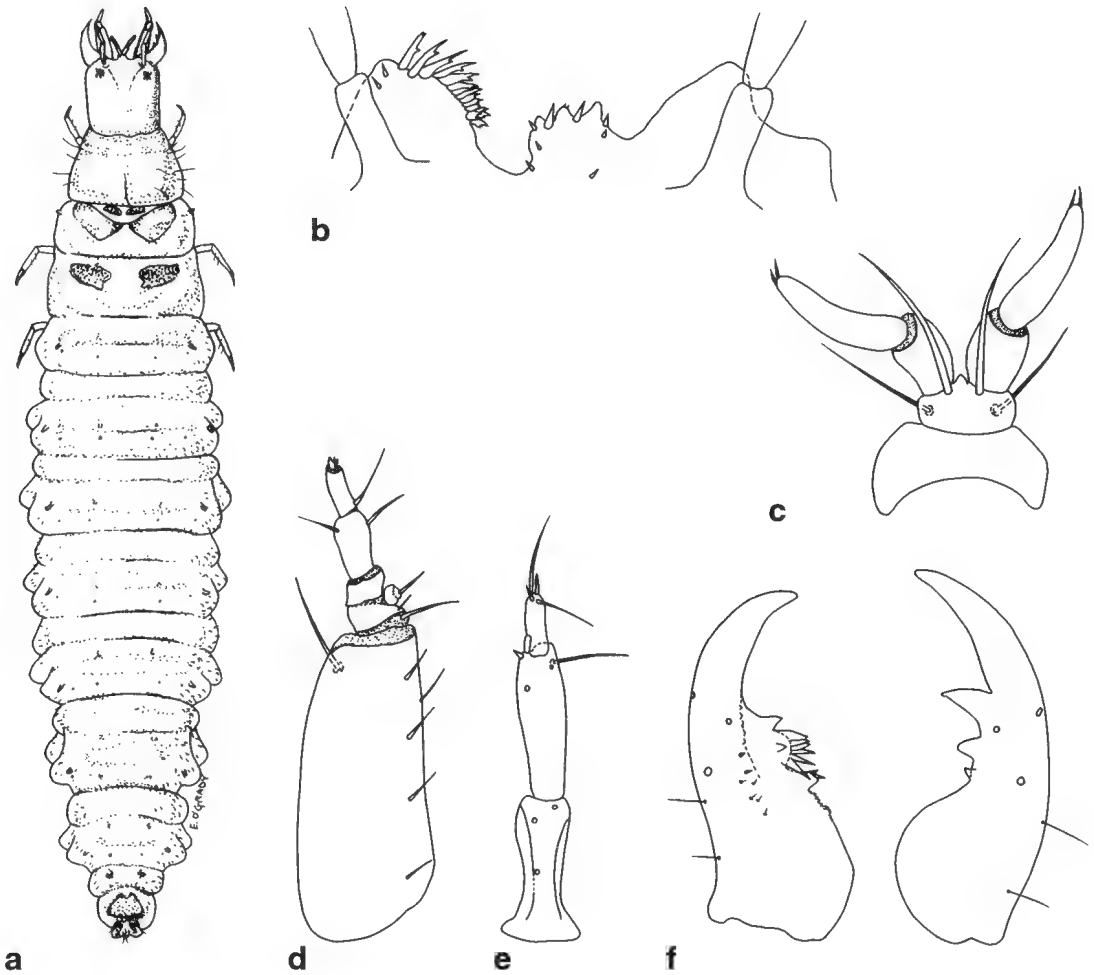


FIGURE 13. *Laccobius decipiens*. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandibles.

Labium. Mentum small and narrow, subrectangular. Prémentum slightly larger, trapezoidal. Palpus two-segmented, first segment shorter, second segment two to three times longer than first. Ligula obsolete, at most reduced to a slight bulge.

Thorax and legs. Prothorax completely covered by a large dorsal sclerite, with sagittal line; ventrally with a pair of large subrectangular sclerites, fused in anterior half. Mesothorax with two pairs of dorsal sclerites, anterior one small, subrectangular; posterior pair larger, subtriangular. Metathorax with one pair of small, irregularly shaped sclerites intermediate in size to the two mesothoracic ones. Legs five-segmented, visible in dorsal view.

Abdomen. Segments 1 to 7 similar in shape, tapering towards posterior end, segments subdivided by transverse folds; sides with several slight bulges, each segment with a pair of long dorsal setae arising from small, darkly pigmented areas, one just behind spiracle and the other near midline. Segment 8 with a subtriangular dorsal sclerite. Segment 9 small, trilobed, bearing a pair of small one-segmented urogomphi. Integument with quite dense covering of short fine setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional, on short dark-pigmented papillae; spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

Within specimens that I have identified as this species there is some variation as follows: some specimens have an additional small third tooth on the right mandible; in newly moulted specimens there are slight serrations on the upper mandibular teeth which appear to wear away quickly; the first abdominal segment occasionally has a pair of very small dorsal sclerites.

Interspecific variation

Within specimens unidentified to species there is variation in the shape of the dorsal sclerites on abdominal segment 8; the width of the nasale and the shape of the nasale teeth; the presence, size and position of abdominal sclerites. Overall these differences are slight.

Identification

By rearing larvae collected in the field.

Specimens examined

New South Wales: Bombala, 28/11/98; ditto, 4/11/97; ditto, 18/1/97. **Victoria:** Stratford, 7/11/97.

Laccobius spp. **Queensland:** Kauri Creek near Tinarro Dam, 24/10/93, col. D. Larson.

Remarks

There is little difference between the larvae of the Australian species and those of the North American *L. minutoides* Orchymont and *L. agilis* (Randall) described and illustrated by Richmond (1920) and Archangelsky (1997).

Limnoxenus Motschulsky*Limnoxenus zealandicus* (Broun). Fig. 14

Size of third instar. Length 11.5–15.0 mm; head capsule 1.60–1.79 mm long, 1.62–2.00 mm wide.

Head capsule. Square. Labroclypeus slightly asymmetrical; nasale moderately developed, angled slightly with right side more forward, with five teeth, left tooth a little distant from others; lateral lobes of epistome rounded, projecting not quite as far as nasale, right lobe often a little more rounded and a little more projected than left lobe. Frontal sulci U to V-shaped, fusing just before reaching occipital foramen. Coronal sulcus very short. Gular sclerite absent. Cervical sclerites relatively small, subrectangular.

Antennae. Three-segmented. First segment longer than remaining segments combined, with

some slender setae on distal two-thirds of inner margin; second segment about twice the length of third segment which is very thin. Sensory appendage on second segment minute.

Mandibles. Symmetrical with three inner teeth, progressively smaller towards base.

Maxillae. Five-segmented. Stipes stout, longer than remaining segments combined, with four long stout setae on inner margin. Palpus four-segmented; first segment the widest, with a short inner process; second and fourth segments short, subequal in length; third segment longest.

Labium. Mentum subrectangular, sides slightly concave, dorsal surface with small spines, anterolateral angles rounded, with several stout spines. Prementum square, not much smaller than mentum. Palpus two-segmented, first segment the shortest. Ligula present, slightly longer than first palpal segment, tip bifid.

Thorax and legs. Prothorax with large dorsal sclerite, with sagittal line; ventral surface with a large subrectangular sclerite, with sagittal line. Mesothorax with a pair of large triangular dorsal sclerites. Metathorax with a pair of wineglass-shaped dorsal sclerites sometimes with stem of wineglass absent. Rest of surface of thorax covered with very short spines, occasionally arranged in short rows. Legs five-segmented, relatively short, barely visible in dorsal view.

Abdomen. First segment with a dorsal pair of small subovoid sclerites close to anterior margin. Segments 1 to 6 similar in shape, tapering towards the caudal end; segments 7 and 8 more elongate and slender. Segments 1 to 7 subdivided into three transverse folds; dorsal surface of third fold with four small, dark, narrowly cylindrical tubercles; sides of each segment with three slight, fleshy bulges. Segment 8 with a large suboval dorsal sclerite, with three to four quite deep indentations on hind edge, lighter coloured towards middle. Segment 9 trilobed, with a pair of short one-segmented urogomphi. Integument densely covered with small setae and a sparse covering of longer setae which get progressively smaller posteriorly. Dorsal surface often with two darker stripes through sclerites and inner pair of tubercles.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional, on small papillae. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

The number of nasale teeth is variable with up

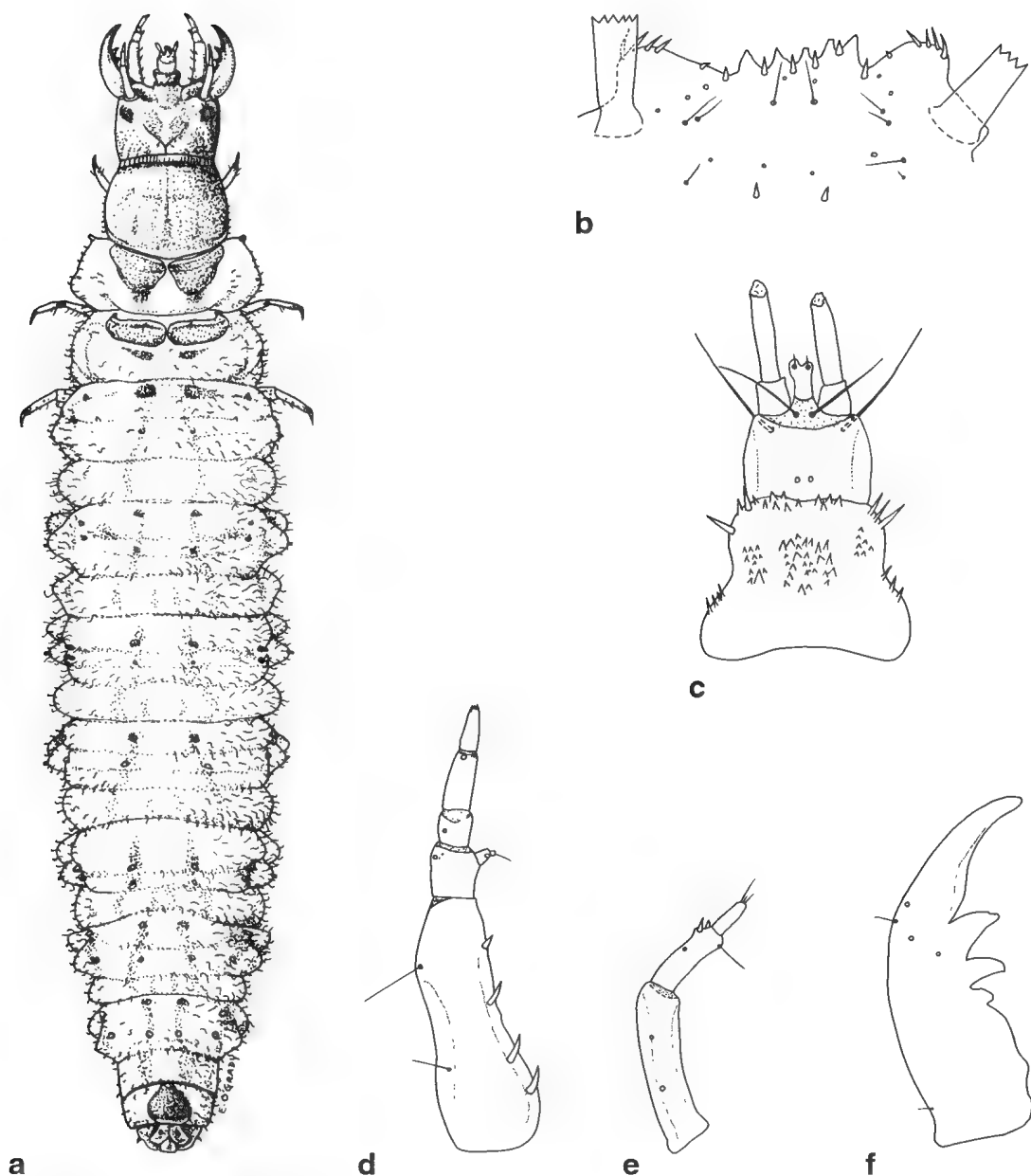


FIGURE 14. *Limnoxenus zealandicus*. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandible.

to ten smaller teeth in some specimens; in some specimens these are worn down to the stage where the front of the nasale is almost smooth. The central nasale teeth are not well developed in first instar larvae. In one specimen the antennae are four segmented with the normal third segments clearly divided into two.

Identification

By rearing from larvae collected in the field.

Remarks

The larva of the European *L. niger* (Gimelin) has already been described by Berge Henegouwen (1975). The larva of the sole Australian and New

Zealand species differs little from those of this species.

One of the most commonly collected hydrophilid larvae in Australia, it is quickly recognised by the parallel darker stripes on the dorsal surface and combination of relatively short basal segment to the antenna and symmetrical three-toothed mandibles. The dense covering of small setae gives the abdomen a fur-like look.

Specimens examined

New South Wales: 10 km E Braidwood, 30/11/95; Braidwood, 19/1/97.

South Australia: 10 km N Coonawarra, 10/11/97; 10 km E Mt Compass, 13/9/97; Mt Crawford Forest, 10/11/96; 6 km N Forreston, 3/10/95; 19 km N Forreston, 3/9/99; 1 km S Nangwarry, 9/10/97; ditto, 29/8/99; 2 km S Penola, 20/11/99; Warburton River, 2–8/10/99, 27°52'23"S 137°54'40"E; Watervally, 7.2 km NNE Mt Rough, 15/10/00. **Tasmania:** Lake St Clair, 4 km N Derwent Bridge, 25/1/00. **Victoria:** 5 km NE Dartmoor, 11/10/97; 2 km W Brimpaen, 23/9/98; Healsville, 12/68; 6 km N Noojee, 16/1/97. **Western Australia:** Gin Gin, 15/10/96; 10 km E Kalamunda, 16/10/96; 2 km W Nannup, 20/10/96; 6 km S Pinjarrah, 23/10/96; 1 km S Serpentine, 24/10/96; 10 km S Yallingup, 22/10/96.

Regimbartia Zaitzev

Regimbartia attenuata (Fabricius). Fig. 15

Size of third instar. Length 5.0–7.5 mm; head capsule 1.00–1.01 mm wide, 0.75–0.80 mm long.

Head capsule. Subquadrangular. Labroclypeus symmetrical; nasale very short, with numerous short teeth on anterior border of epistome; lateral lobes of epistome rounded, very short, not projecting as far as nasale, each with two long setae. Frontal sulci straight, short, meeting at about the level of the antennal bases. Coronal sulcus long, about half the length of the head capsule. Gular sclerite absent. Cervical sclerites small, subrectangular.

Antennae. Three-segmented. First segment slender, longer than other two combined, with a prominent subapical inner process some distance from apex. Sensory appendage on second segment slim, slightly shorter than third antennal segment.

Mandibles. Virtually symmetrical, long and slender, with two inner teeth on basal half; distal tooth large, basal one small.

Maxillae. Five-segmented. Stipes slender, much

longer than remaining segments combined, with four or five setae on inner margin. Palpus four-segmented; third segment longest; second segment shortest; first and fourth segments subequal in length, first segment with a short inner process.

Labium. Mentum large, wider than long, sides convex, dorsal surface with cuticular spines. Prementum elongate, much narrower than mentum. Palpus two-segmented, basal segment short. Ligula annular, two to three times as long as basal segment of palpus.

Thorax and legs. Prothorax with a large dorsal sclerite, with sagittal line; surface covered by minute spines; fringe of long, slender setae around the margins, four small spines, one on each anterolateral angle and two towards the middle; ventral surface with large, subrectangular sclerite, without sagittal line. Mesothorax with two dorsal pairs of subtriangular sclerites; metathorax with one dorsal pair of irregular shaped sclerites. Both mesothorax and metathorax with five pairs of setiferous projections, about half of them with a narrow cylindrical projection with a long seta attached at the end. Legs five-segmented, long, visible from above.

Abdomen. Segments 1 to 7 with five pairs of setiferous projections similar to those on thorax, four lateral ones with one more posterior than others and one closer to midline. In addition, the abdomen is covered with small stellate setae and the dorsal surface with small projections each with six to eight long, sharply pointed setae (in most specimens these structures are obscured by an accumulation of sand grains and detritus). Segment 8 without setiferous projections, with a pair of small finger-like 'proceri', with dorsal semispherical sclerite which covers the spiracular atrium. Segment 9 trilobed, with a pair of small, unsegmented urogomphi.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Interspecific variation

There is little variation between the few specimens seen.

Identification

By association of adults and larvae by isoenzyme electrophoresis.

Remarks

The larvae closely resemble both *Allocotocerus*

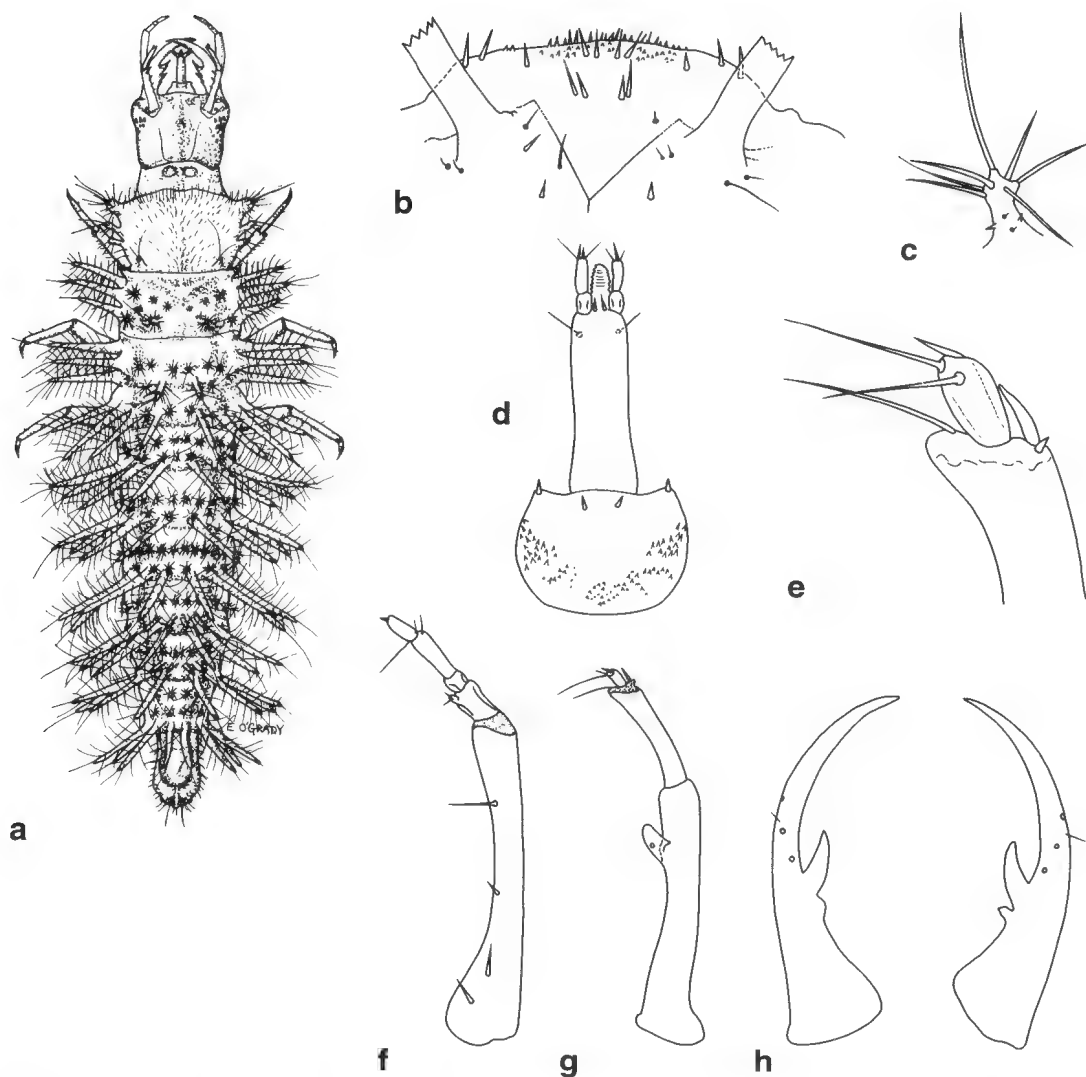


FIGURE 15. *Regimbartia attenuata*. a, habitus; b, labroclypeus; c, labium; d, detail of abdominal stella; e, tip of antenna; f, maxilla; g, antenna; h, mandibles.

and the New World *Derallus* (Archangelsky 1997; Spangler 1966), all three genera showing a suite of unusual characters that clearly separate them from other Hydrophilid larvae. The differences between the genera are relatively slight (see key and under *Allocotocerus*).

Specimens examined

Queensland: 6 km N Bluewater, 3/2/97; 15 km W Mareeba, 6/12/90, col. D. Larson; 5 km NW Mareeba, 22/9/90, col. D. Larson; 2 km N Mt Molloy, 1/4/96.

Sternolophus Solier

Sternolophus marginicollis (Hope). Fig. 16

Size of third instar. Length 11.5–15.0 mm; head capsule 1.80–1.90 mm long, 1.55–1.70 mm wide.

Head capsule. Subrectangular. Labroclypeus weakly asymmetrical; nasale short, weakly projecting with five short teeth, left one a little distant from rest; lateral lobes of epistome symmetrical not projecting beyond nasale, undulating. Frontal sulci V-shaped, fusing before

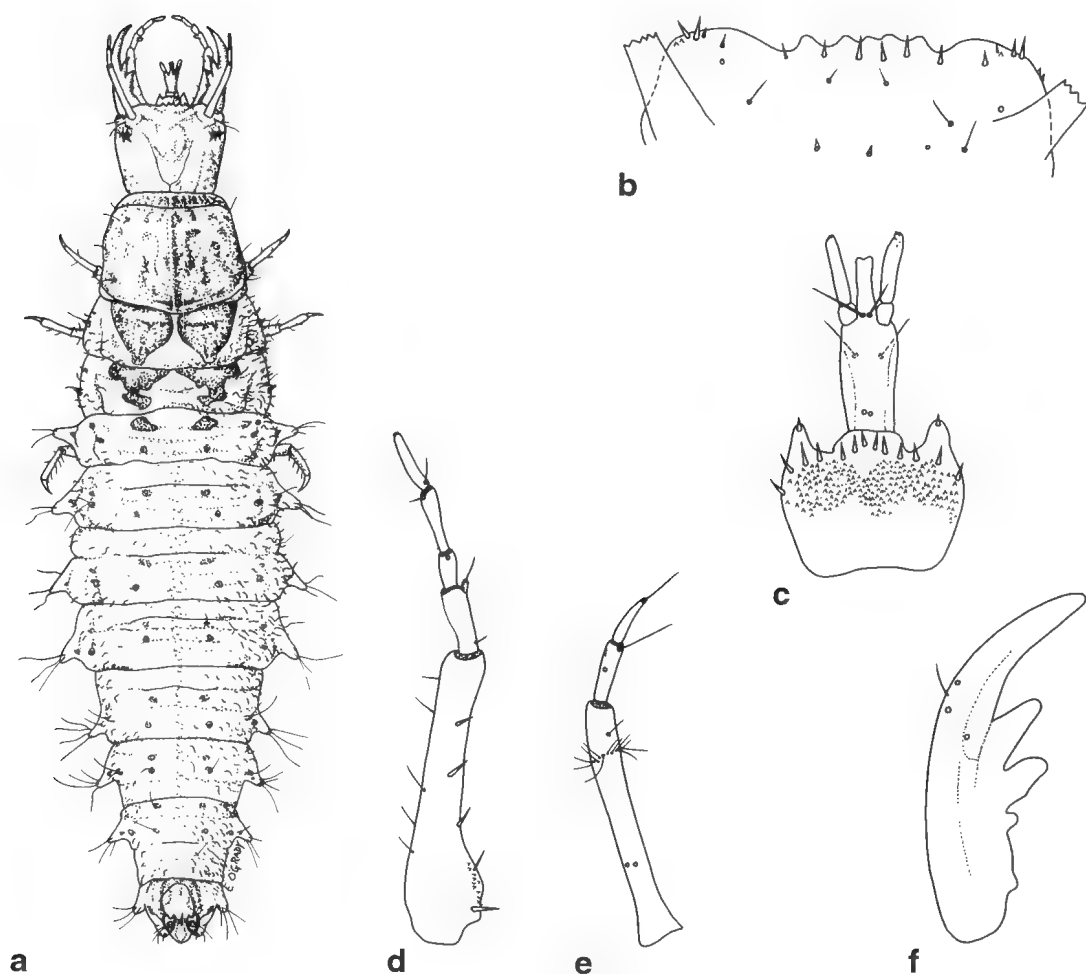


FIGURE 16. *Sternolophus* sp. a, habitus; b, labroclypeus; c, labium; d, maxilla; e, antenna; f, mandible.

reaching occipital foramen. Coronal sulcus short. Gular sclerite absent. Cervical sclerites small, suboval, longitudinally oriented. Frontal sulcus outlined in a darker colour.

Antennae. Three-segmented. First segment much longer than other two combined, with an annular ring of long setae near apex in second and third instars; second segment and third segment subequal. External apical appendage on second segment lacking; a small flat button-like structure on outside towards apex.

Mandibles. Virtually symmetrical, with three inner teeth, distal two large, basal one much smaller.

Maxillae. Five-segmented. Stipes as long (first instars) or longer (second and third instars) than

remaining segments combined, with four or five setae on inner margin and patch of small spines on inside near base. Palpus four-segmented; first segment with an inner apical process; second segment short; third and fourth segments a little shorter than first.

Labium. Mentum with sides convex, slightly wider than long, anterolateral corners pointed, dorsal surface with numerous small cuticular spines and row of longer spines towards apex; small spines mostly absent in first instar. Prementum long and thin. Palpus two-segmented, basal segment much shorter than distal. Ligula a little shorter than distal segment of palpus, slightly bifid at tip.

Thorax and legs. Prothorax with large dorsal

sclerite, with sagittal line, with pattern of darker lines and dots; ventral surface with a large subrectangular sclerite, with sagittal line. Mesothorax and metathorax each with a dorsal pair of subtriangular sclerites, smaller than those

of prothorax. Legs five-segmented, long, visible in dorsal view, with rows of long swimming-setae on femur and tibiotarsus.

Abdomen. Segments 1 to 6 similar in shape, tapering towards the caudal end; segments 7 and 8

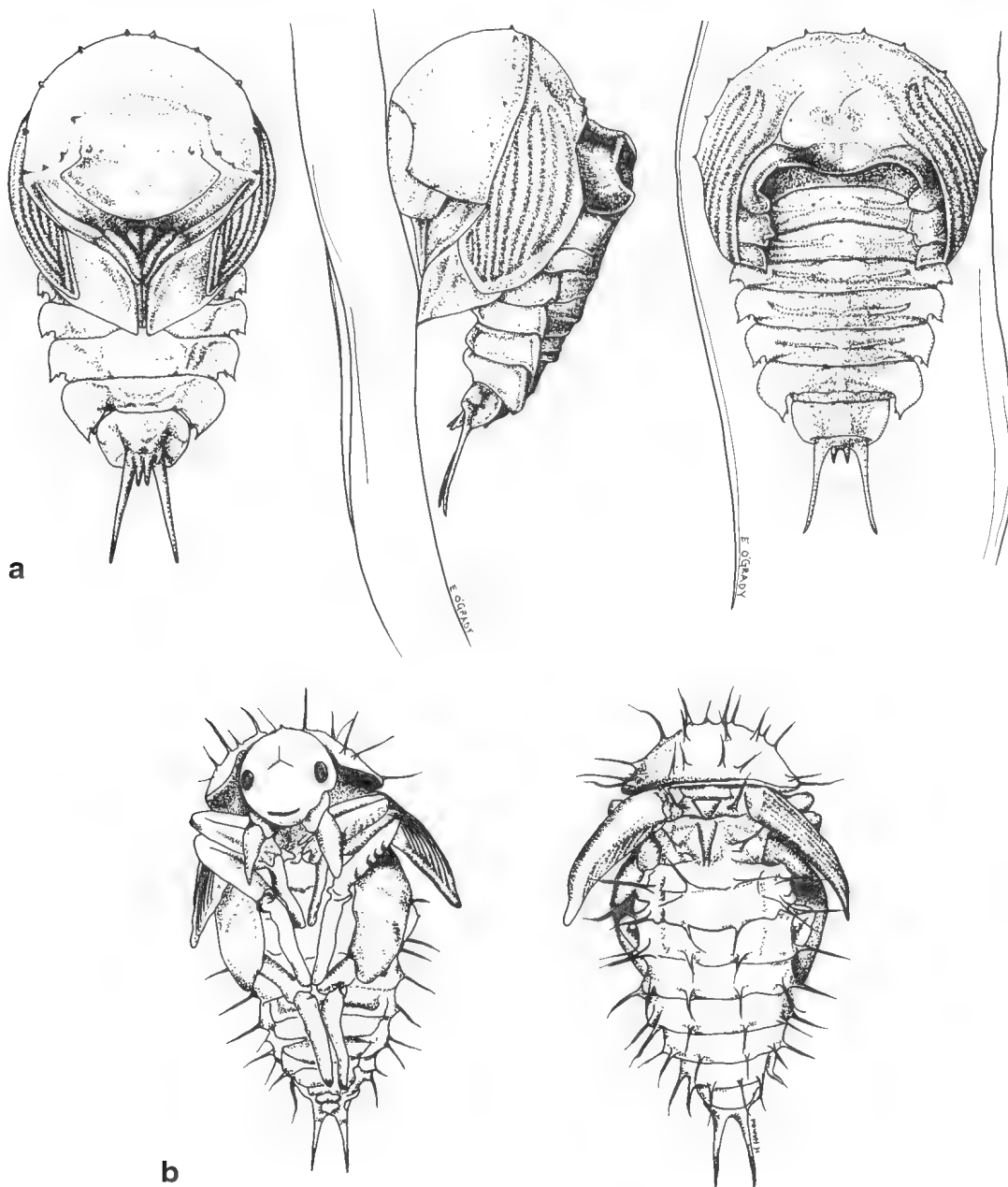


FIGURE 17. a, *Amphiops queenslandicus*: ventral, lateral and dorsal views of pupa. b, *Hybograllius hartmeyeri*: ventral and dorsal views of pupa.

more elongate and slender. Segments 1 to 7 subdivided into three transverse folds, each segment with transverse row of six pairs of long setae arising from short dark-pigmented cylindrical bases on dorsal surface of posterior fold. Pleura 1 to 8 each with a small, lateral, setiferous tubercle. Segment 8 with two small, dorsal, subtriangular sclerites at posterior end. Segment 9 slightly trilobed, with a pair of short one-segmented urogomphi. Integument densely covered with both very short and moderately long setae.

Spiracles. Nine pairs; one mesothoracic and eight abdominal. Mesothoracic and first seven abdominal spiracles non-functional. Spiracles on segment 8 annular, large and functional, within the spiracular atrium.

Intraspecific variation

There is some suggestion of two longitudinal dark lines on the dorsal surface in some specimens, and in an occasional specimen the small third mandibular tooth is virtually absent.

Interspecific variation

In some specimens of *Sternolophus* there is a greater development of the lateral abdominal tubercles into quite prominent finger-like projections, especially towards the rear; a row of setiferous papillae across the abdominal segments instead of small cylinder-like structures; a more symmetrical nasale; a stronger third mandibular tooth; and some difference in the shape of the meso and metathoracic sclerites (the habitus drawing (Fig. 16) is of this form). These larvae are *S. centralis* Watts and/or *S. immarginatus* Orchymont. The distribution of specimens would suggest the latter but not certainly so.

Identification

By rearing from field-collected larvae.

Remarks

The larva of *S. marginicollis* is one of the

few Australian larvae already known (Bertrand 1935) as *S. tenebricosus* Blackburn, a junior synonym (Watts 1989), although the identification was by association, which is unsafe in this genus because it often has two or more species common at the same locality. Other species have been described from Africa and Japan (see Bertrand 1972). The present larvae, certainly of *S. marginicollis* and probably also including *S. immarginatus* Orchymont, do not differ significantly from the published descriptions and illustrations.

Larvae of *Sternolophus* are commonly encountered in Northern Australia and can be readily separated from other Hydrophilid larvae by the combination of long thin prementum, long ligula and mandibles with three teeth.

Specimens examined

Northern Territory: Jabiru, 19/3/98; Manton Dam, 2/2/99; Ormiston Gorge, 27/1/99. **Queensland:** Killymoon Creek, 25 km S Townsville, 2/2/97.

Sternolophus sp. **Northern Territory:** Holmes Jungle near Darwin, 28/1/99. **Queensland:** 8 km N Bluewater, 31/10/95; Bohle River, 10 km N Townsville, 23/3/96; Eubenangee Swamp, 4/2/97; 2 km S Mt Molloy, 30/3/96.

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I wish to thank Mr Rod Gutteridge, Ms Eloese O'Grady and Mr Harold Hamer for so ably preparing the illustrations; Dr David Larson for donating larvae he collected whilst working in North Queensland; the South Australian Library staff, Ms Marianne Anthony and Ms Jill Evans, for procuring references that we did not already have in the library; and Ms Debbie Churches for preparing the final manuscript copy. I would particularly like to thank Dr Steve Donnellan of the Evolutionary Biology Unit of the South Australian Museum for undertaking the biochemical matching of adult and larval *Allocotocerus* and *Regimbartia*.

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EMBOLOCEPHALUS YAMAGUCHI (BRINKHURST, 1971) (CLITELLATA: TUBIFICIDAE) FROM SOUTH AUSTRALIAN STREAMS

A. M. PINDER & P. K. McEVOY

Summary

Papillate tubificids from streams in the Mount Lofty Ranges are identified as *Embolocephalus yamaguchii* (Brinkhurst, 1971) and represent the first records of this largely Holarctic genus from Australia. Collection details are provided for records of a second papillate species, identified as belonging to the genus *Spirosperma*.

**EMBOLOCEPHALUS YAMAGUCHII (BRINKHURST, 1971) (CLITELLATA: TUBIFICIDAE)
FROM SOUTH AUSTRALIAN STREAMS**

AM PINDER & PK McEVOY

PINDER, AM & McEVOY, PK. 2002 *Embolocephalus yamaguchii* (Brinkhurst, 1971) (Clitellata: Tubificidae) from South Australian streams. *Records of the South Australian Museum* 35(2): 139–145.

Papillate tubificids from streams in the Mount Lofty Ranges are identified as *Embolocephalus yamaguchii* (Brinkhurst, 1971) and represent the first records of this largely Holarctic genus from Australia. Collection details are provided for records of a second papillate species, identified as belonging to the genus *Spirosperma*.

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Most tubificids with papillate body walls are contained within a complex of genera (including *Embolocephalus* Randolph and *Spirosperma* Eisen) established, or re-established, following revision of the genus *Pelosclex* Leidy (Brinkhurst 1991; Brinkhurst & Wetzel 1984; Holmquist 1978, 1979). These genera have a largely Holarctic distribution, with few records from southern continents. The latter consist of a record of the otherwise European *Embolocephalus velutinus* (Grube, 1879) from Venezuela (Dumnicka, 1983), an identification questioned by Brinkhurst and Marchese (1989), and papillate tubificids of uncertain identity from Peru (Brinkhurst & Marchese 1989). The North American species *Quistadrilus multisetosus* has been recorded as far south as Mexico. In Australia, Timms (1978) recorded *Pelosclex* (*sic*) from a lake in Tasmania and Pinder & Brinkhurst (1994, 2000) noted papillate tubificids from Victoria and New South Wales. The latter were all immature so descriptions were not possible, but they were tentatively assigned to *Spirosperma*, based on the presence of papillae and the form of the chaetae. Collection details for this species, including the first records from South Australia, are presented below for the first time. Other specimens, collected from streams in the Mount Lofty Ranges in South Australia, are herein described and identified as *Embolocephalus yamaguchii* (Brinkhurst, 1971), a species otherwise known only from Lake Biwa in Japan.

METHODS

Serially sectioned specimens were cut at 6 µm and stained in haematoxylin and eosin. Measurements were taken using an eyepiece graticule on a Zeiss Jenamed 2 compound microscope calibrated with an Olympus stage micrometer. Abbreviations used in the line-drawings are a: atrium, cp: cuticular pad, e: large epidermal papillae, ed: ejaculatory duct, ff: female funnel, mf: male funnel, p: prostate, pe: penis, sa: spermathecal ampulla, sc: spermathecal chaeta, scg: spermathecal chaetal gland, v: vas deferens. Specimens are either in the senior author's collection (AP) or the Australian Water Quality Centre collection (AWQC); returned to WSL Consultants (WSL) or Australian Water Technologies (AWT); or deposited with the South Australian Museum (SAM) or the Museum of Victoria (NMV).

SYSTEMATICS

Embolocephalus Randolph, 1892

Type species

Embolocephalus velutinus (Grube, 1879)

Diagnosis

From Holmquist (1978) and Brinkhurst (1981). Prostomium and sometimes first segments retractable within the rest of body. Body wall with epidermal papillae, generally concealed by a

secreted layer with embedded foreign particles. Hair chaetae present dorsally, usually broad and sabre-like, with pectinate crotchet chaetae. Bifid and/or simple pointed chaetae present ventrally, usually both in anterior bundles. Spermathecal chaetae modified on X, lying in a well-developed chaetal sac. Male ducts each with a long winding vas deferens, usually narrower entally and broader (up to twice the width) ectally, entering the atria apically. Atria long and tubular to crescentic, broadest near the prostate union, tapering to a short ejaculatory duct. One large prostate gland joining each atrium towards the middle of the latter. Penes well developed without thickened cuticular sheaths. Spermathecae with ovoid to oblong ampullae, well set off from the ducts, with pores usually more or less in front of and lateral to the spermathecal chaetal sacs.

Distribution

Europe, North America, Japan, Kamchatka, ?Venezuela and now Australia.

Embolocephalus yamaguchii (Brinkhurst, 1971)

Peloscolex yamaguchii Brinkhurst, 1971: 505

Peloscolex sp. Yamaguchi, 1953: 295

Embolocephalus yamaguchii (Brinkhurst, 1971) Ohtaka, 1994: 52; 1995: 174

Material examined

South Australian specimens. SAM E3095–3101: 3 mature specimens serially sectioned, 3 mature dissected and 1 immature whole-mounted, Aldgate Creek at Strathalbyn Road, Mylor, tributary of the Onkaparinga River (AWQC site 3217), 35°02'S 138°45'E, samples E33, 3 June 1997 and F32, 27 Oct 1997. AP: 1 mature serially sectioned, collected as above. SAM E3102–3103: 1 mature in alcohol, Onkaparinga River at Houlgraves Weir (AWQC site 3205), 35°05'S 138°43'E, sample E37, 3 June 1997, and 1 mature whole-mounted from same site, sample F37, 28 Oct 1997. SAM E3104: 1 mature in alcohol, Aldgate Creek at Aldgate Valley Road (AWQC site 13022), 35°02'S 138°45'E, sample H41, 2 Dec 1998. AWQC: 5 immature in alcohol, Onkaparinga River at Hack Bridge (AWQC site 3212), 35°03'S 138°45'E, sample H43, 1 Dec 1998. AWQC: 1 immature in alcohol, Lenswood Creek at gauging station (AWQC site 3208),

34°56'S 138°50'E, sample OCB148, 17 Jul 2000: AWQC: 2 mature in alcohol, Onkaparinga River at Silver Lake Road (AWQC site 13023), 35°04'S 138°45'E, sample OCB181, 17 Oct 2000. Collections by V. Tsymbal, P. McEvoy, A. Lang and S. Wade (Australian Water Quality Centre, South Australia).

Japanese specimens. From collection of A. Ohtaka (Hirosaki University, Japan): 1 mature specimen serially sectioned, 1 mature whole-mounted and 2 mature in alcohol (now dissected), Lake Biwa, Japan.

Habitat

This species has been collected only from a sixth order reach of the Onkaparinga River upstream of Mount Bold Reservoir and from two fourth order tributaries, between 245 and 295 metres above sea level. Specimens were collected from both riffle and edge habitats, with substrates ranging from those composed mainly of bedrock, boulder or cobble to those dominated by finer sediments and/or detritus. Willow root mats are a common feature on the stream bed of most sites. Riparian zones had an overstorey of either indigenous *Eucalyptus* species and *Acacia melanoxylon* and/or introduced willows (*Salix* spp.). Land uses include grazing, horticulture and urban settlement. Apparently similar habitats in adjacent catchments were sampled with the same sampling intensity without finding *E. yamaguchii*.

Description of Australian specimens

Length of preserved specimens 15.6–25.5 mm, width at clitellum 0.7–1.1 mm. Each pre-clitellar segment with a band of tall, broad epidermal cells forming a raised transverse ridge in the middle of the segment, pronounced dorsally and laterally but virtually absent ventrally. Body surface with foreign material adhered to elongate ovoid papillae covering the entire body except for the clitellum (Fig. 1). Papillae mostly 15–22 µm long on pre-clitellar segments (measured on the longest axis, including foreign particles) and 20–34 µm long on post-clitellar segments, and mostly 17–25 µm high (with most of the height constituted by the foreign material). Ridges of anterior segments with fewer or no papillae. Each segment also with 2 rings of papillae that are taller and broader than normal (up to 40 µm wide and 40 µm high including foreign material), which give the appearance of darker (or sometimes lighter) bands around each segment, 1 ring about at the level of the chaetae and 1 anteriorly on each segment, most pronounced on posterior segments.

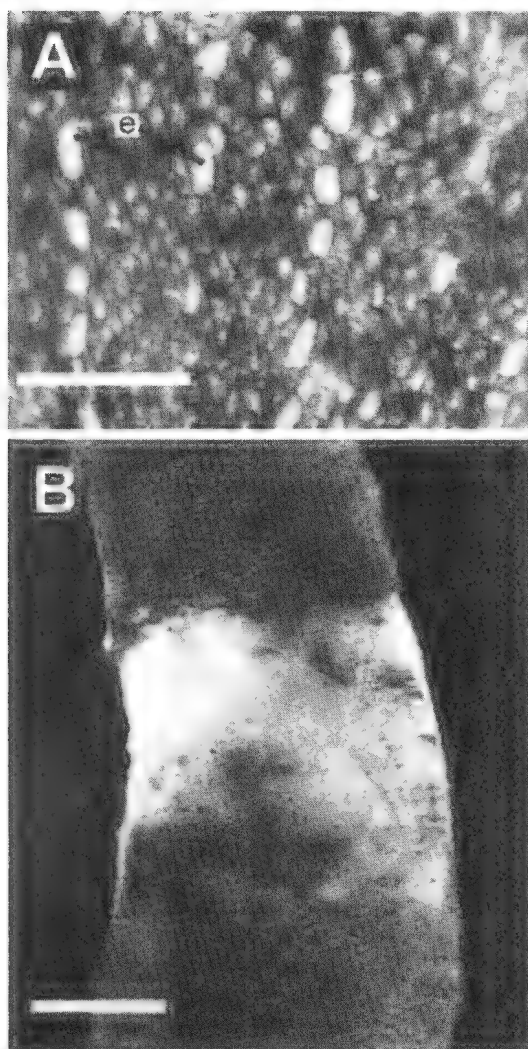


FIGURE 1. *E. yamaguchii* A, Enlarged view of body wall of segments towards the posterior end of SAM E3098 (prior to slide mounting) showing normally sized and enlarged (e) papillae; B, Portion of SAM E3104 showing lateral view of anterior segments (top), clitellum (centre) and post-clitellar segments (bottom). Scale bar for A 100 μ m, B 500 μ m.

Other (possibly sensory) papillae present with the foreign material adhered only to the sides, with the top of the papillae exposed, arranged in ill-defined rings around each segment (about 10 of these papillae per ring), usually 1 ring at the level of the chaetae and 1 or more rings between the chaetae and intersegmental furrow. These partially naked papillae are about the same size as the

shorter type of fully encased papillae and are sometimes visible as darker or paler spots. A pad of tall, thin epidermal cells, with cuticle 10 times thicker (up to 17 μ m) than elsewhere, present medially on the spermathecal segment, adjacent to the anterior spermathecal chaeta. Clitellum covering posterior half of X and all of XI, paler than other segments due to a smooth even coating of soft white granular material (Fig. 1).

Prostomium partially retracted into first segment in fixed animals. Pharynx with dorsal muscular pad in II to III, with pharyngeal gland cells on pharynx and on septa 3/4 to 4/5. Oesophagus from IV to VI, widening into broader thicker-walled intestine in VII.

Ventral chaetae 130–211 μ m long and 7–14 μ m wide at nodulus, generally smallest in pre-clitellar bundles. Ventral bundles on II to VIII usually with 1 bifid and 1 simple pointed chaeta, rarely 1 extra bifid chaeta and/or 1 or 2 extra simple pointed chaetae. Bifid chaetae with teeth equal in width but upper tooth up to 1.5 times longer than lower (Fig. 2B). Posterior ventral bundles with 1 (rarely 2) bifid chaetae, with upper teeth becoming shorter than lower and lower tooth greatly expanding in width and becoming notably recurved (Fig. 2C). Dorsal chaetal bundles normally with 2 to 4 slightly curved hair chaetae, 220–420 μ m long and 4–7 μ m wide, with finely plumose shafts and blunt, slightly swollen, tips, with an equivalent number of short (32–75 μ m long and 1–2 μ m wide) finely pectinate crotchets with thin parallel outer teeth (Figs 2D,E). Posterior dorsal bundles with fewer of both types of chaetae. Chaetae of spermathecal segment modified (Figs 2A, 3A,B), ventral chaetae absent in XI.

Genitalia paired (Figs 2, 3B). Testes anteroventral in X, ovaries anteroventral in XI. Male funnels large, ciliated vasa deferentia broad near funnels (35 μ m), narrowing shortly thereafter (17–20 μ m) and widening slightly ectally (25–33 μ m), highly coiled, joining ental end of atria. Atria each with a narrow lumen and layer of tall glandular lining cells, crescentic, broadest where a single prostate gland joins (slightly entad of medial), tapering at either end, the ectal end forming a short ejaculatory duct which enters the penis apically. Atrial muscle layer thin, wider where prostate joins. Atrium, including ejaculatory duct, measuring 800 x 110 μ m to 1000 x 185 μ m. Prostate glands voluminous, sometimes ballooning into following segment. Penes broad entally, narrowing at about one-third of the distance from the tip to form a narrower ectal end,

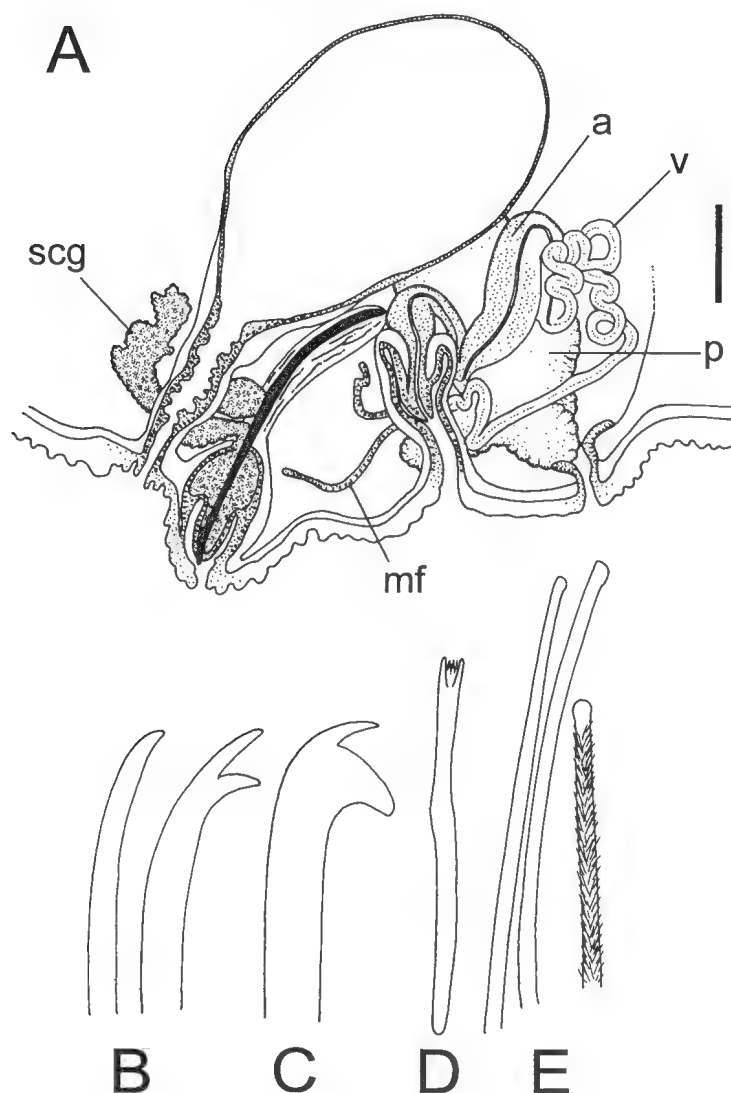


FIGURE 2. *E. yamaguchii*. A, Reconstruction of genitalia (with organs drawn in the same plane for simplicity) from serial sections of SAM E3095; B, tips of anterior ventral chaetae; C, tip of posterior ventral chaeta; D, dorsal pectinate chaeta; E, tips of dorsal hair chaetae, with plumosity shown for one hair. Scale bar for A 200 μ m.

penes within thin-walled muscular penis sacs attached to the dorsolateral body wall by numerous muscle fibres. Penes and penis sacs with cuticle no thicker than on body wall (ie without penis sheaths). Male pores in line with ventral chaetae on anterior half of XI, within a common transverse depression of the ventral body wall. Spermathecal ampullae variable in size (770–1350 μ m long), each containing 1 or 2 long thin spermatozeugmata (length of only one whole

spermatozeugmata measured, 660 x 45 μ m, but others 80 μ m wide in cross-section, indicating greater length). Spermathecae with stout ducts (300–370 μ m) that are constricted ectally, leading to pores anterior on X slightly medial to line of ventral chaetae. Spermathecal chaetae long (510–670 μ m) and thin (10 μ m) with grooved tips, ectal half lying in well-developed chaetal sacs. The sacs tall (220–300 μ m) and muscular, with inner lining tissue that can be everted with the tip of the chaeta

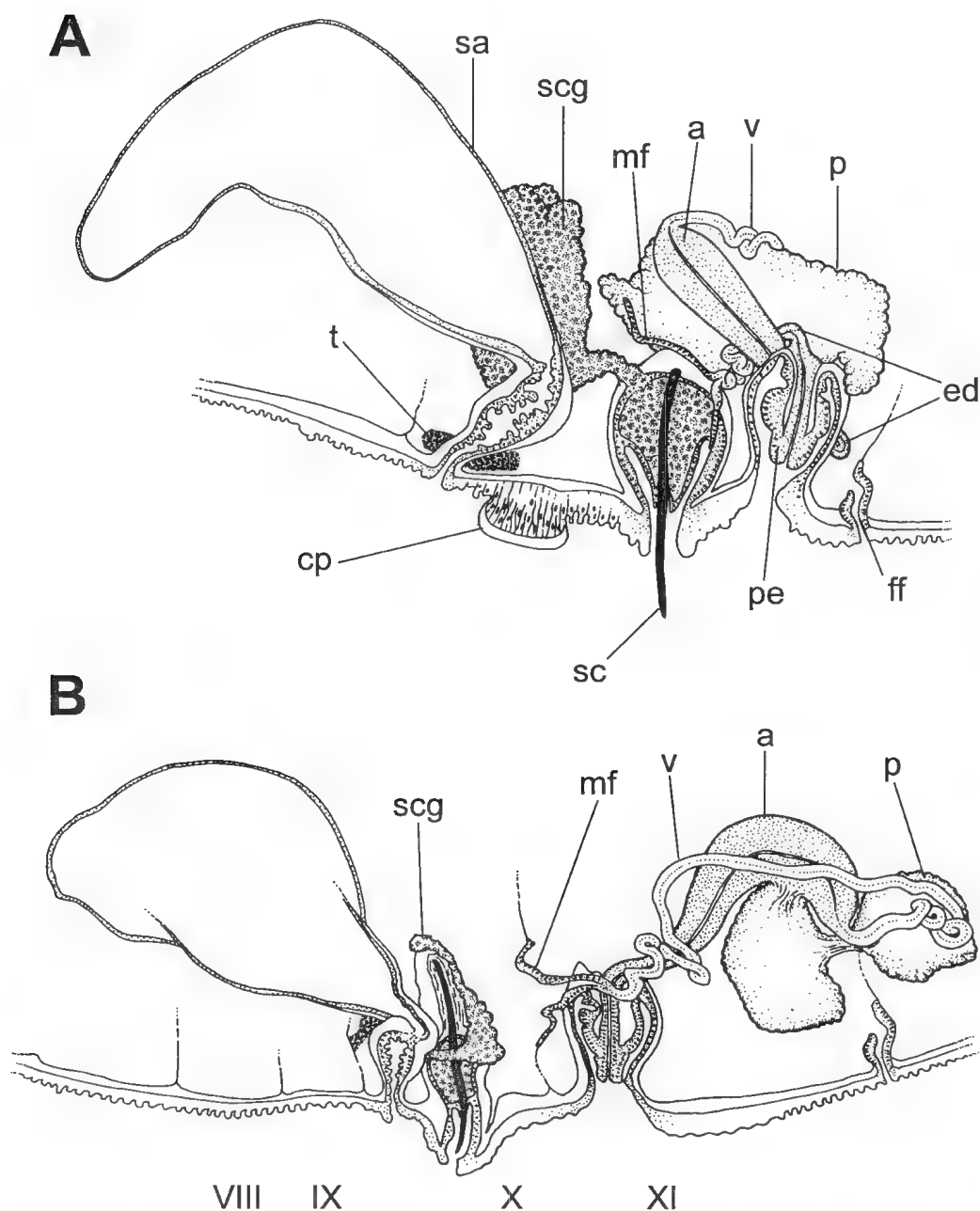


FIGURE 3. *E. yamaguchii*. Reconstruction of genitalia (with organs drawn in the same plane for simplicity) from serial sections of A, SAM E3096 and B, SAM E3097. Scale bar for A 200 μ m.

to form a large papilla and with muscular layer extending to cover the ental end of the chaeta. Sacs with a gland attached dorsally, varying in extent of development (between and within individuals). Spermathecal chaetal sacs located asymmetrically,

both opening slightly ventral to the line of somatic ventral chaetae, 1 immediately posterior to spermathecal pore on one side and the other close to 11/12 in front of the sperm funnel on other side. Female funnels posterolateral on XI.

Remarks

The presence of simple-pointed chaetae on segments II to VIII, separate openings for the spermathecal ducts and spermathecal chaetae, dorsolateral ridges on anterior segments and asymmetrical location of the spermathecal chaetae clearly ally these Australian specimens with the Japanese species *E. yamaguchii* rather than with any of its congeners. We initially considered that the Australian specimens were either conspecific with *E. yamaguchii* or represented a very similar sister-species. The latter was seen as more likely since *E. yamaguchii* is known only from Lake Biwa in Japan and other *Embolocephalus* seem to have fairly restricted Holarctic distributions. However, a thorough comparison of *E. yamaguchii* (from the description in Ohtaka 1994 and material seen by us) and the Australian specimens led to the conclusion that there was no morphological justification for a new species description. The only differences between the Australian and Lake Biwa specimens are the size of the worms and the size of some genital organs. None of the Australian specimens reach the maximum length of 35 mm measured for the *E. yamaguchii* neotypes (Ohtaka 1994), but most Lake Biwa specimens are less than 30 mm (Ohtaka pers. comm.). The vasa deferentia of the Australian specimens are narrower than those (20–24 μ m wide entally, 40 μ m ectally) recorded for *E. yamaguchii* by Ohtaka (1994) and the ectal portion is not so enlarged relative to the ental portion. However, the vasa deferentia of Lake Biwa specimens measured by us (as narrow as 13 μ m entally to a maximum of 25 μ m ectally) more closely match measurements from the South Australian material. Other components of the genitalia (atria, spermathecal ampullae and spermathecal chaetae) are slightly larger in the Australian specimens than recorded by Ohtaka (1994). The raised epidermal pad was not noted for *E. yamaguchii* by Ohtaka (1994) but was present on Lake Biwa material seen by us and is visible in Fig. 4B of Ohtaka (1994). This feature is not known for other *Embolocephalus* species.

These specimens represent the first records of this species and genus in Australia and one of the few records of the genus from southern continents. The known distribution of this species (Lake Biwa in Japan and the Mount Lofty Ranges in South Australia) is exceptional within the Australian tubificid fauna. Other tubificids found in Australia are either endemic or cosmopolitan (occurring in most, if not all, other continents).

?*Spirosperma* sp.

Material examined

All specimens immature. WSL consultants voucher AN30: 2 in alcohol, Old Namoi River at Bullerawa Station, (Duncan's Junction) New South Wales, 30°18'05"S 149°04'00"E, 27 Jun 2000. AWT: 1 specimen, Georges River at Cambridge Avenue, New South Wales, 33°58'S 150°54'E, 1 Apr 1996; 1 specimen, Peach Tree Creek, at Weir Reserve, New South Wales, 33°45'S 150°41'E, 17 Jul 1996; 1 specimen, Second Ponds Creek downstream of Rouse Hill Sewage Treatment Ponds, 33°40'S 150°55'E, 1 Apr 1996. AP: 1 whole-mounted on slide, Plenty River at Lower Plenty, Victoria, 37°44'S 145°06'E, 10 Apr 1994, coll. S. Schreiber (formerly Monash University); Glenelg River at Rocklands, Victoria, 37°14'S 141°57'E, 3 Jun 1994, coll. S. Schreiber. NMV F81865: 1 in alcohol, LaTrobe River at Moe-Willow Grove Road Bridge, Victoria, 38°11'18"S 146°15'12"E. NMV F81864: 1 in alcohol, Curdies River, Victoria, 38°20'S 143°08'E, 7 Feb 1992, coll. G. Quinn (formerly Monash University). AWQC voucher 5665: 1 in alcohol, Pilby Creek outlet (AWQC site 13095), South Australia, 33°59'S 140°53'E, 24 Nov 1998, coll. D. Schulze and T. Venus.

Brief description

Prostomium retractable within mouth. Body wall densely papillate, with foreign material

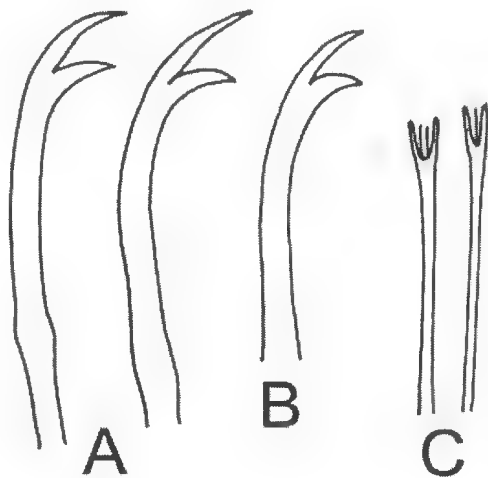


FIGURE 4. *Spirosperma* sp. A, ventral chaetae of anterior to mid-body segments; B, ventral chaeta of posterior segment; C, tips of dorsal crotchet chaetae.

attached to most papillae. Some papillae with foreign matter on lateral walls only. Without rings of distinctly larger papillae. Ridges of enlarged epidermal cells absent on anterior segments. Ventral chaetae (Fig. 4) all bifid, 3 to 6 per bundle, with upper teeth 2 to 3 times as long as lower teeth in anterior and mid-body segments, 1.5 times as long as lower teeth in posterior segments (Fig. 4). Ventral chaetae of first few segments usually slightly longer and thicker than the rest. Dorsal bundles with 1 to 3 smooth hair chaetae and 1 to 3 very small crotchet chaetae with finely bifid ends and 1 or 2 intermediate teeth (Fig. 4).

Remarks

This species lacks simple-pointed chaetae anteriorly and so has been tentatively identified as a *Spirosperma* rather than an *Embolocephalus*, but mature specimens are required to confirm the generic affiliation. It appears to be widespread in rivers of southeastern Australia.

ACKNOWLEDGMENTS

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EARLY ABORIGINAL FISHING TECHNOLOGY IN THE LOWER MURRAY, SOUTH AUSTRALIA

PHILIP A. CLARKE

Summary

The early Aboriginal fishing technology of the Lower Murray region of South Australia is described and compared with other areas in south-eastern Australia where fish was a dominant dietary component of hunters and gatherers. This is a study of cultural geography, the chief concern being a description of hunting and gathering techniques and their significance to Aboriginal occupation of the landscape.

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The early Aboriginal fishing technology of the Lower Murray region of South Australia is described and compared with other areas in south-eastern Australia where fish was a dominant dietary component of hunters and gatherers. This is a study of cultural geography, the chief concern being a description of hunting and gathering techniques and their significance to Aboriginal occupation of the landscape.

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INTRODUCTION

Aboriginal fishing technology in the Lower Murray region is discussed from the pre-European period to the early years of European settlement. A major aim is to describe how hunting and gathering techniques used by Lower Murray people made their region culturally distinctive (Fig. 1).¹ This region is defined as the area from Cape Jervis in the west, east to Wellington on the Murray River and south to Kingston, taking in the whole of the Lower Lakes, Coorong and associated coastal belt. It is estimated that just prior to European settlement, the region supported a population of 5000 Aboriginal people, although this figure was probably seriously affected by two early waves of smallpox (Brown 1918: 230; Campbell 2002: 119–133; Clarke 1994: 57–63; 1995: 156, footnote 1; Gale 1969). The descendants of these people, many of whom still live in the region, generally call themselves Ngarrindjeri (Berndt & Berndt 1993; Clarke 1994; Hemming & Jones 2000; Jenkin 1979).²

In the Lower Murray region the Murray River flows from Murray Bridge to Lake Alexandrina

through an open valley cut across a very low and flat limestone karst plain, which is less than 30 metres above sea level (Fenner 1931: 81–83; Twidale 1968: 148–149, 383–384). Below Wellington, the river becomes two large lakes (Alexandrina and Albert) and a series of channels in the form of a delta, eventually exiting behind scattered islands at the Murray Mouth.³ Here, the river meets the Coorong, which drained the South East region of South Australia before European intervention.⁴ The sea, winds and tides combine to drive the river back with heavy sand dune systems, called Sir Richard and Younghusband Peninsulas (northwest and southeast parts, respectively).⁵ From the point of view of the early Aboriginal inhabitants, the delta of the Lower Murray provided the region with many kilometres of shoreline for hunting and gathering activities.

The climate of the Lower Murray region is influenced by the powerful ‘controls’ of its temperate latitude, the proximity of the sea and the relief of the land (Fenner 1931: 125; Howchin 1909: 142; Penney 1983: 85–93; Schwerdtfeger 1976: 75–86). Upstream, long sections of both the Murray River and its main tributary, the Darling

¹ Hunting and gathering practices in the region since the 1940s are discussed elsewhere (Clarke 2002).

² The Ngarrindjeri (= Narrinyeri) were formerly made up of descent groups who spoke one of several dialects, such as Ramindjeri, Yaraldi (= Jarildekald) and Tangani (= Tanganekald).

³ Lake Alexandrina is called ‘Lake Victoria’ on some early official maps (Cockburn 1984: 7).

⁴ The Coorong was formerly known as the ‘South East Branch’ in reference to Lake Alexandrina, which it joined at Pelican Point (Cuique [R. Penney] in the *South Australian Magazine*, September 1842, vol. 2: 18–23).

⁵ Due to the action of the ocean currents, the location of the river exit into the sea is constantly moving; at present it is migrating northwards towards Goolwa at the rate of several metres per year (F. Tuckwell, pers. comm.). The complete disappearance of Barker Knoll at the Mouth as early as 1859 (Linn 1988: 78) indicates that some movement is a natural feature.

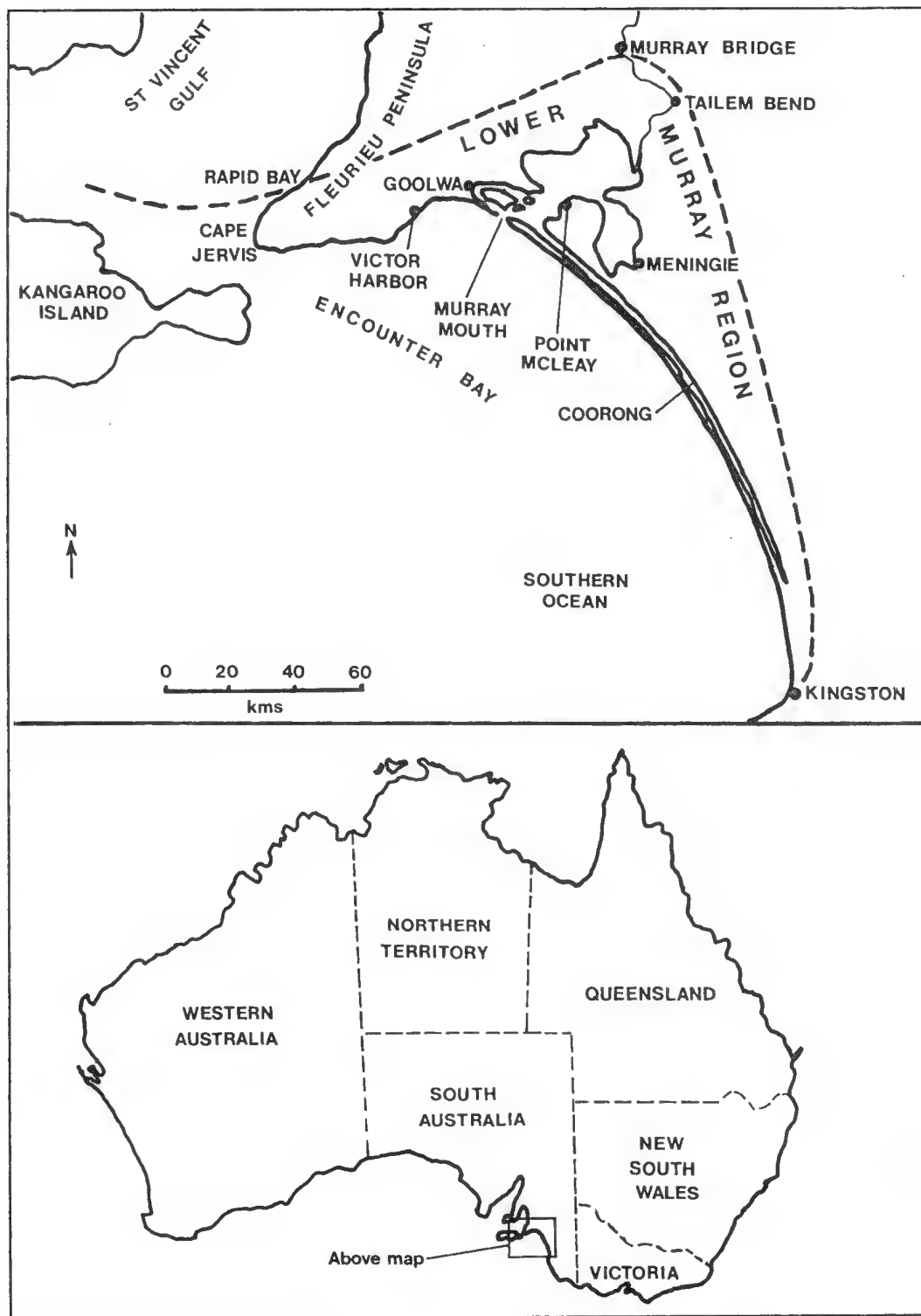


FIGURE 1. The Lower Murray cultural region.

River, flow through semi-arid regions. Nevertheless, the Lower Murray region is entirely contained within the high rainfall area of South Australia, receiving 350–750 mm per year. It comes under the rainfall shadow of the Mount Lofty Ranges to the west, with precipitation also increasing near the coast. Annual average temperature throughout the region is less than 18°C, with the greatest range of temperatures being during the summer months (Fenner 1931: 65, 126; Griffin & McCaskill 1986: 50–51; Laut et al 1977).

SOURCES OF ABORIGINAL ENVIRONMENT USE DATA

The literature of Aboriginal hunting and gathering technology for the region is based on four main sources of data — the archaeological record, the historical ethnographic record, scientific analysis of the properties of naturally occurring substances and contemporary research with Aboriginal people. This paper deals mainly with historical ethnographic sources of information, which includes artefacts collected from living people. Archaeological investigations provide evidence of the importance of fish in the diet of coastal/riparian Aboriginal groups, with an indication of the material cultural items and the main species fished.⁶ Biological analysis of human bone also assists in determining the pre-European diet (Pate 1997, 1998, 2000). Scientific methods of analysis of food sources, such as those determining the pharmacological and nutritional properties, can illustrate their potential human uses. The literature investigating the usefulness of Australian fish as food and medicine includes Brand Miller et al (1993: 222–223), Clarke (1989: 3) and Isaacs (1987: 153–164). Nevertheless, cultural perceptions influence the potential use of plants and animals, with not all available resources being fully utilised. To understand how Lower Murray Aboriginal people used their environment, and thereby moulded their cultural landscape, we must at present rely primarily on records made by early European observers, supplementing this with ethnographic data from contiguous riparian/coastal regions.

Although useful data on pre-European plant use, such as species identification, method of use and seasonality, can be obtained from

contemporary fieldwork with Aboriginal people, there are significant post-European changes in Lower Murray Aboriginal culture and in the physical landscape itself. For instance, information received from Lower Murray Aboriginal people in recent times on bush foods used during the last 50 to 60 years indicates far less use of roots than before (Clarke 1988: 64). In contrast, other indigenous foods such as fish, waterfowl, kangaroos, emus and berries continued to be used in restricted contexts. Nevertheless, the introduction of foreign species, such as European carp, and environmental changes in the waterways have decreased numbers of some Australian fish species. The availability of European-type foods, especially flour, potatoes and canned foods, obtained from missions, farm stations and towns led to a decline in many indigenous food sources. The decrease in 'bush food' consumption was particularly marked for those species requiring significant labour expenditure. Other foods were replaced by European varieties with more favourable properties. The bulrush root, for example, contains a great deal of fibre that makes eating difficult. Unlike earlier Aboriginal foods, many European sources were available at all times of the year because they were imported.

The detailed recording of Aboriginal culture in the Lower Murray region started with the German Heinrich A. E. Meyer, who ran a mission at Encounter Bay during the late 1830s and early 1840s (Meyer 1843, 1846). From him we obtain a Ramindjeri-speaker's view of Lower Murray culture. The Englishman George Taplin established an Aboriginal mission at Point McLeay on the south-western shore of Lake Alexandrina in 1859. In the 1870s he published two main books on Ngarrindjeri (= Narrinyeri) culture, based on records in his journals (Taplin 1859–79, 1874, 1879). Taplin used Ramindjeri sources as a guide to his research, although local Aboriginal groups living around Point McLeay were mainly Yarlaldi-speakers. He described people who were feeling the impact of European expansion and the considerable changes it had brought upon them and the Lower Murray landscape, particularly at the northern end. One of Taplin's initiatives to improve their circumstances was to establish a local fishing industry for Aboriginal people at the mission (Jenkin 1979: 97–98, 110–111).⁷

⁶ For an archaeological overview of the Lower Murray / South East districts, see Campbell (1934, 1939, 1943), Campbell et al (1946), Luebbers (1978) and Pretty et al (1983).

⁷ There are many entries in Taplin's journals concerning the establishment of the fishing industry. The important references are 21 September 1859, 18 October 1859, 25 November 1859, 22 December 1859, 11 January 1860, 7 February 1860, 15 February 1860 and 1 March 1860.

Adding to the missionary records in the 19th century are the recordings of colonists such as George French Angas (1847a, 1847b), William A. Cawthorne (1844 [1926]), Dirk M. Hahn (1838–39), Richard Penney (1840–43)⁸ and William Wells (1852–55). During this century, various anthropologists studied Lower Murray Aboriginal culture: Ronald M. Berndt (1940; with Catherine H. Berndt 1993), Alison Harvey (1939ms, 1943) and Norman B. Tindale (1930–52, 1931–34, 1934–37, 1935, 1937, 1938, 1938–56, 1941, 1981, 1987; with Mountford 1936; with Pretty 1980). Their accounts are rich in detail concerning past hunting and gathering practices, filling many gaps that were left in the early historical record. They also contain examples of post-European innovations by indigenous people. Largely due to the interests and efforts of the Director of the South Australian Museum, Edward C. Stirling, and Ethnology Curator, Norman B. Tindale, the South Australian Museum possesses a large collection of early artefacts from the Lower Murray region.⁹ In the 1980s the present author commenced studying Aboriginal relationships to the physical landscape (Clarke 1985a, 1985b, 1986a, 1986b, 1987, 1988, 1989, 1994 chapter 4, 1998, 1999b, 2001a). The region and Aboriginal relationship to it also featured in the Hindmarsh Island Bridge controversy (Bell 1998; Stevens 1995; Wilson 1998). The attention that scholars have directed towards the Lower Murray has meant that it is ethnographically one of the best-described regions in southern Australia. The biases within this literature are discussed elsewhere (Clarke 1994 section 11.3, 1999a: 149–151, 2001a: 19–20).

EARLY ABORIGINAL FISHING TECHNOLOGY

In the pre-European period the high Aboriginal population along the river frontage and the coastal zone of South Australia was in sharp contrast to the sparse population in the interior. In the Murray Basin region the distribution of people was estimated to be 0.4–0.5 square kilometres for each

individual, in contrast to 31–88 square kilometres required in Central Australia (Jones 1974: 326; Lawrence 1968: 72–73; Maddock 1972 [cited Rose 1987: 22–23]; Meggitt 1962 [cited Abbie 1976: 46–47]; Smith 1980: 68–90; Tindale 1981: 1860). It has been demonstrated that the physical environment of the Lower Murray formed both a natural and cultural region (Clarke 1994). Stable isotope research on human bone indicates that, in general, neither people nor foods were moving from the Murray Bridge area to the adjacent Murray Mouth and Coorong (Pate 1998). The Lower Murray therefore formed a separate hunting and gathering region. Nevertheless, some aspects of the material culture and natural resource use by Aboriginal people here was similar to that of riverine and coastal communities described from elsewhere in Australia (Hallam 1975; Lawrence 1968: 85–122; Lourandos 1997: 195–243).

In the 1930s Tindale mapped many of the favourite fishing places and lookouts in southern South Australia, from informants such as Louisa Eglinton (Narangga woman), Milerum (Clarence Long, Tangani man) and Albert Karloan (Yaraldi man).¹⁰ In the Tangani language, elevated areas used as ‘watch places’ were called *popaldi*, whereas in Ramindjeri they were *koinkoinj*.¹¹ Older men generally used these when looking out for fish shoals and bird movements, as well as for monitoring the movements of their neighbours by observing the smoke from their campfires. In comparison to adjacent regions, such as the Murray Mallee and Mount Lofty Ranges, the Lower Murray landscape offered Aboriginal people abundant opportunity to make fish a more significant food source.

Before the arrival of Europeans, Aboriginal people in southern Australia did not widely use the fishhook and line (Curr 1883: 110; Davies 1881: 129; Eyre 1845, vol. 2: 266–267; Massola 1956; Meyer 1846 [1879: 192]; Olsen 1991: 5).¹² Nevertheless, the use of bone bi-points or fish gorges (*muduk*) and fishing lines has been recorded from along the Murray River (Flood 1999: 48; Gerritsen 2001; Pretty 1977: 321–322). Similar items have been recorded from the

⁸ Newspaper articles by Richard Penney between 1840 and 1843 are reprinted in the *Journal of the Anthropological Society of South Australia* 1991: 1–107.

⁹ From 1988 to 1999, a major exhibition on Aboriginal culture in the Lower Murray, called ‘Ngurunderi, a Ngarrindjeri Dreaming’, was open at the S.A. Museum (Hemming & Jones 2000).

¹⁰ Tindale Aboriginal Site Maps of southern South Australia, South Australian Museum Archives, Adelaide. Also see Tindale (1935–60: 15).

¹¹ Tindale (no date, ‘Milerum’, Stage A, #9, Archives, South Australian Museum, Adelaide).

¹² Tindale (1934–37: 285) recorded a description by Karloan (Karlowan) of fishhooks being made from bone, gum and stick, but this was possibly a post-European development.

Gippsland and Geelong areas of southern Victoria (Smyth 1878 vol. 1: 391). Shell fishhooks have also been recovered from coastal shell middens in eastern Victoria (Mulvaney & Kamminga 1999: 292).

After Europeans arrived, Aboriginal people in the Murray River and Lower Murray regions adopted new fishing techniques and appeared to have made their own version of the fishhook.¹³ In 1938 Tindale recorded Albert Karloan who said:

Our fish hook was made from a bone of a kangaroo tied like a real fish hook to another piece which was the point but our old folks used the fish spear all the time; nothing was as good as the real fishing spear! We walked along the banks & got fish in the reeds (Tindale 1930–52: 42).

European twine, hooks and lines were also handed out at the Point McLeay Mission (Taplin Journals: 18 September 1862). Fishing techniques used in the Lower Murray region included netting, spear and club fishing, trapping and opportunistic collecting.

NET-FISHING

The Ngarrindjeri people referred to the act of netting fish as *ngerin* (Taplin 1879: 130). Marine net fishing often involved the coordination of a large number of people. Worsnop provided a vivid account of Aboriginal people sea fishing in the 19th century. He records:

In Encounter Bay I have seen the natives fishing almost daily. Two parties of them, each provided with a large net, square in form, with a stick at either end, and rolled up, swam out a certain distance from the shore, and then spread themselves out into a semicircle. Every man would then give one of the sticks round which his piece of net was rolled to his right hand man, receiving another from his left hand neighbour, bringing the two nets together, thus making a great seine. They now swam in towards the shore, followed by others of their number, who were engaged in splashing the water and throwing stones, frightened the fish and prevented their escape from the nets (Worsnop 1897: 90–91).

George French Angas painted two men fishing

with a seine net at Second Valley, south of Adelaide, in 1844 (Angas 1847a: Plate XXI). Cawthorne provides a similar scene, in watercolour, at Second Valley, dated c.1842 (figure in Hemming & Jones 2000: 9), as does Snell in his sketches, dated 14 July 1850, at Yorke Peninsula (Snell 1849–59 [1988: 128]). Eylmann (1908: 375 & Plate XXXIV fig. 3) published a drawing of two Ngarrindjeri men using a long seine net, with a third man helping to drive the fish in. It is likely that several nets were sometimes connected together with supporting sticks.¹⁴ In situations where nets were not available, branches could be used to drive the fish up on the beach (Angas 1847b: 112). A former colonist wrote to Tindale stating that in the Port Germein area, north of Adelaide:

On occasions a wall of prickly bushes was built in about three feet [one metre] of water and rolled shorewards, the ends converging to an arc. The fish which were impaled or caught were extracted by the pushers and thrown to others following behind (Parkes 1936, cited in Tindale 1935–60: 48).

The 'wall' of branches, comprised of saltbush and mangrove, was called *winda* and required two people to roll it and two more for picking out the fish (Parkes 1936, cited in Tindale 1935–60: 96).

Net fishing in fresh water required fewer people than sea fishing, with small nets used to catch fish living amongst reeds and logs. Nets were essential items of Lower Murray material culture for fishing in the lagoons of the Lower Lakes, Coorong, Murray River and in the creeks of the southern Fleurieu Peninsula. In the Encounter Bay area, Aboriginal women also caught tadpoles from claypans with fine meshed nets and cooked them in large 'mutton-fish' shells (Worsnop 1897: 83).

There was some degree of specialisation in the nets used by Lower Murray people. Harvey (1943: 111) described three main types of nets used by Yaraldi-speaking people of the Lower lakes. Nets with a small mesh, *jatrumi* [pronounced 'yatrumi'], were used when fishing for *kanmuri* (mullet, *Aldrichetta forsteri*). The nets with a larger mesh, *neri*, were used for *tukkeri* (bony bream, *Nematalosa erebi*). The big drum nets, *dongari*, were mainly for catching *pondi* (Murray cod, *Maccullochella peelii*) found under large logs

¹³ In 1932 Tindale (1953: 42) recorded from a European named Arthur White that Aboriginal people living along the river had used a double-pointed wooden fishhook. Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide) also claimed that they used a fishing toggle made from bone as a form of fishhook.

¹⁴ This technique was also used in southern Yorke Peninsula (Tindale 1936: 57).

submerged in the river.¹⁵ The drum nets were made with sticks in the form of a rectangular pouch (Harvey 1943: 111).

The Tangani people of the Coorong used specialised nets, such as the *jataruma* [pronounced 'yataruma'] to catch mullet and the *donggari* to catch mulloway (*Argyrosomus hololepidotus*) and other big fish (Tindale 1934–37: 226). They also used the *ngeiri* net, which was made from the same sedges that were collected for basket and mat making. All nets used by Tangani people in the pre-European period were for hauling (Tindale 1934–37: 226). The Tangani used a hooped fishing net, termed *kandaranguku*, with a mesh of 2.5 cm, for larger fish (Tindale 1951: 258). Apparently the term is a play on words meaning 'widow catcher', as *kandari* is applied to coarse rope and *rangku* refers to a widow.¹⁶ Murray River people around Moorundie used the same type of net, *kanderunku*, to catch *ponku* (Murray cod).¹⁷ The Kingston people used a net called *pinang kanji* to round up fish in shallow waters (Tindale 1931–34: 89). Angas provided a small watercolour painting of a pouch-like net 'for taking very small fish from Lake Bonney' (Angas 1847a: Plate LI) in the South East of South Australia.

Aboriginal people in southern South Australia probably did not use set nets until well after European settlement. Tindale's main Lower Murray informant, Clarence Long (Milerum), claimed that set nets were rarely used in the Coorong when he was younger, and not at all before then (Tindale 1934–37: 226). This suggests that Europeans had introduced the practice to the local Aboriginal people. From available accounts, sinkers and floats were not used in association with net fishing during the pre-European period of southern South Australia. The record of Murray River people using clay from wasp nests to make sinkers for set nets is probably a post-European innovation.¹⁸ Tindale (1935–60: 17) suggested that vegetation placed along the top of the net to prevent fish from jumping out of the water might have helped keep the net vertical.

It is likely that in the pre-European period most

fishing nets in southern South Australia and Victoria were fabricated from two-ply string made from fibre obtained from the roots and stems of the bulrush (*Typha* species) (Beveridge 1883: 42; Kreff 1862–65: 361; Tindale 1935–60: 17; Zola & Gott 1992: 8–9, 62). Europeans also know this plant as flag, cumbungi and reed mace, whilst contemporary Ngarrindjeri people refer to it as *manangeri* or *manakeri* (Clarke 2001b). It was a major food source, with the chewed remains of the roots being generally in good supply in Aboriginal camps (Clarke 1988: 69–70, 72; Tindale & Mountford 1936: 497). Tindale stated that:

... mature rhizomes were chewed and fibres made into string, the chewing for this purpose being a duty of women. Older women's teeth were often worn to the gum line by their constant chewings.¹⁹

He also suggested that the proximity of bulrush grounds would have made a good riverside camp.

In 1894 an Aboriginal man from Point McLeay, Jacob Harris, provided a detailed written account of net making from 'rushes', which were probably bulrushes. He said that before Europeans arrived, Aboriginal people in the Lower Murray region used to:

make our nets almost the same as the Europeans did, the meshes were the same, the only difference being that yours [Europeans] were made of twine etc., while ours from rushes. The rushes had to be steamed or cooked or whatever you like to call it, first a hole was dug, say a couple of ft. [= 60 cm], then a fire was placed in it, after it had burned almost to ashes some damp or wet grass was put on the coals, then the rushes, so that the steam arising from the grass would steam or cook ... put in about evening and left until morning, it was then taken out and divided among the camp to chew or suck the juice out of it, which is very sweet, it was then made or twisted into a line for to be made into a net. ... the meshes were the same [as European nets].²⁰

Angas stated that the marine fishing nets were 'composed of chewed fibres of reeds, rolled upon

¹⁵ Descendants from the Yaraldi and Maraura people from the Lower Lakes and Murray River regions made S.A. Museum drum net, A21338, in 1934.

¹⁶ Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide).

¹⁷ Tindale, 'Ngaiawung vocabulary', Archives, South Australian Museum, Adelaide. Also see Scott (cited Tindale 1951: 258).

¹⁸ Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide).

¹⁹ Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide).

²⁰ J. Harris letters (D6510(I))14,15, Mortlock Library, Adelaide). Tindale (1934–37: 164) received a similar description of the process from his Ramindjeri informant, Reuben Walker.

the thigh, and twisted into cord for the purpose' (1847a: Plate XXI).²¹ Emu oil was sometimes rubbed into the fibre while it was being made into two-stranded cord (Tindale 1931–34: 60). Fibre treated in this manner makes the string more supple, while maintaining its strength and durability. Tindale (1951: 257) maintained that Aboriginal cordage from all areas of Australia was always composed of single or two-ply twists, never three or more. Nevertheless, there were exceptions. For instance, West (1999: 20, 23–28) describes the making of three-ply rope in Arnhem Land and possibly Tasmania.

After European settlement, changes in the Aboriginal diet would have led to a significant decrease in the availability of fibre from bulrush roots. Fibre used by Lower Murray people to make string for nets also came from an unidentified plant known in the local Aboriginal language as *calgoonowrie* (MacPherson, no date: 10). A plant recorded as used for making Coorong nets was *kuka* (native flax, *Linum marginale*).²² In 1932 an informant from the Maraura people of the Upper Murray of South Australia, Frank Fletcher, said that gill nets and drag nets were both made from the *pungur* rush (Tindale 1953: 23).²³ Harvey (1943: 109–110, 112) stated that the stems of *jalkeri* (knobby club rush, *Isolepis nodosa*) were used for making nets.²⁴ But field investigations have indicated that the stems of this rush are pithy and not suitable for making string or baskets. The stems of *mangatu* (spiny sedge, *Cyperus gymnocaulos*) would have been better; this species is still used by local Aboriginal people who make baskets and mats from it.²⁵ Nets made from sedge stems were also made for dry uses, such as catching ducks.²⁶

The technique used to make nets in southern South Australia has been variously described as

'knotted netting' or 'knotted looping' (Davidson 1933: 257–259, 269–272, figs 1, 9–10; West 1999: 30–33, 49). The Tangani people called the mesh of the net, *mandar*, which reputedly meant 'the eyes'; the netting knot or tie was *mulbakan* and the act of making a net was *lagulun* (Tindale 1934–37: 226). The last term is a reference to the threading motion of making the knot being like 'spearing'.²⁷ In the Ramindjeri language of Encounter Bay, *lakk-in* was recorded as 'spearing; weaving (as rushes for a basket)' (Meyer 1843: 74). The mesh sizes for nets in southern South Australia were variable, in the range 1–2.5 cm with the Kongarati Cave fragments, 2.5 cm recorded for the Coorong hoop net and 8 cm for netting wrapped around a desiccated body found at Fromm Landing, Murray River.²⁸

SPEAR AND CLUB FISHING

During the day, men caught fish such as *malawe* (mulloway, *Argyrosomus hololepidotus*) by standing motionless in the river or in their canoes (Hemming & Jones 2000: 9; Meyer 1846 [1879: 192–193]; Smith 1930: 230–231; Snell 1849–59 [1988: 182]; Tindale 1934–37: 7). Fishers attracted the fish by their shadows and stabbed them with hand-held spears. Large spears made from *Callitris* pine with two to three wooden prongs lashed to the head were used for spearing mulloway and Murray cod.²⁹ Being large, these spears were also used as punting poles when fishers were travelling on bark canoes and rafts (Hemming & Jones 2000: 9). It is likely that these spears were hidden near the area of their use when the fishing season was over. In the Lower Lakes area fishermen frightened fish from their hiding places by a large noise, created by thrusting one

²¹ A supporting reference is Angas (1847b: Plate LVI). An example of a net made from *Typha* fibre is A2000, collected from the Lower Lakes district.

²² Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide).

²³ The term *pungur* may relate to the *pungguriko* specimen of *Juncus* species collected by Tindale from Swan Reach, 5 August 1964 (A68584, South Australian Museum). If so, then the plant referred to for net-making was probably of the same species. Similarly, a related term, *puungort*, is a Western Victorian Aboriginal term for the basket sedge, *Carex tereticaulis* (Robson 1986).

²⁴ This plant was formerly known as *Scirpus nodosus*.

²⁵ Examples of River Murray fishing nets made from sedges (*Cyperus* species) in the South Australian Museum include specimens A17529, A21338, A26250, A45090. The term *mangatu* was recorded from Aboriginal sources in the 1980s (Clarke 2001b).

²⁶ See figure in Hemming & Jones (2000: 13). Satterthwait (1986: 39–40) provided an overview of the use of nets for catching waterfowl in Aboriginal Australia.

²⁷ In the Ngarrindjeri language of the Lower Lakes, *lakelun* was recorded to mean 'spearing' (Yallop & Grimwade 1975: 33–34, 85–86).

²⁸ Tindale (1951: 258) reported on specimens A65091, A25351 and A20616, respectively. Smyth (1878: 389–390) discussed mesh sizes for Victorian nets.

²⁹ In 1936 Tindale collected a 3.1 m-long fishing spear (Museum specimen A26093) made of pine from the Coorong. This specimen has two prongs lashed to the head and was called *punkularipuri ma:wantj* in the Tangani language. In 1844 G. French Angas painted a close-up of a large spear with three prongs lashed on (Angas collection, Archives, South Australian Museum, Adelaide — see Angas 1847b: Plate XXX). This watercolour is reproduced in Hemming & Jones (2000: 9).

of these pronged spears into the water (Unaipon 1924–25 [2001: 19]). The compressed air caught between the prongs rose to the surface with a loud report. There is an account of spear-fishing competitions held from November to April among the Piltindjeri group of Yaraldi-speaking people living along the southeastern shore of Lake Alexandrina, with the fish caught being presented to senior people in the community (Smith 1930: 231–236; Unaipon 1924–25 [2001: 19–24]). In this instance, it required skill in fish tracking, involving the detection of movements in pondweed, reeds and water ripples.

At night, a fire was used to attract fish to be struck by spear or club (Angas 1847b: 112). Angas painted a club called a *wadna*, which was 'used by the Port Lincoln natives, to throw at fish whilst swimming' (Angas 1847a: Plate LI). Similar bent elongated clubs from the Lower Murray are also in the Museum collection. Clubs like these and described as boomerangs were reported as used along the Coorong (Olsen 1991: 5). Sometimes a bark canoe was used as a platform to fish from, with a fire contained by a clay hearth in the middle that also served to cook the catch (Angas 1847b: 54, 101, 107; Meyer 1846 [1879: 193]).³⁰ Mobility across water was important for the fisherman in order to reach areas favoured by particular species of fish. Therefore, rafts made from reed stems (*Phragmites australis*) and grass-tree flower-stalks (*Xanthorrhoea* species) would also have been important items of fishing material culture in the Lower Lakes and along the river lagoons.³¹ Although relatively common along the Murray River and in the Lower Lakes, bark canoes were rarely seen in the Coorong lagoon, and even then only for bringing in trade items.³² Red gum trees (*Eucalyptus camaldulensis*) required for bark are found only in permanent freshwater regions, such as along creeks in the southern Fleurieu Peninsula and along the Murray River. There is no evidence that any form of watercraft was ever used for sea fishing, although short trips were made on reed rafts or floats to nearby rocky islands in order to kill seals there (Tindale 1941: 241).

OPPORTUNISTIC HARVESTING

There are documented cases of Aboriginal use of fish poisons in small lagoons of the upstream reaches of the Murray River bordering northern Victoria (Curr 1883: 110). Nevertheless, Taplin doubted that Ngarrindjeri people possessed knowledge of the use of poisonous plants (Taplin 1879: 47). When large numbers of fish died for natural reasons, such as changes in salinity in the river or lake, Aboriginal people quickly gathered them (Eyre 1845, 2: 266). Before the construction of the barrages across the Murray Mouth separating the Coorong from Lake Alexandrina, elderly Aboriginal informants interviewed in the 1980s claimed that there were sometimes rapid changes in the water from fresh to saline (Clarke 2002). This tended to kill a large number of fish, providing an abundant but temporary source of food. At other times, the incoming salt water drove certain species, such as Murray cod, upstream and suspended fishing in the lakes until it receded (Olsen 1991: 8; Taplin Journals: 19 May 1860). Bony bream also die off seasonally in large numbers and, according to Ngarrindjeri informants in the 1980s, they had provided a temporary windfall of food (Clarke 2002).

FISH-TRAPS AND ENCLOSURES

Fish-traps and enclosures ranged from slight modifications to natural features of the landscape to special purpose-built structures (Mulvaney & Kamminga 1999: 34–35). For example, in some areas Aboriginal people were able to use the narrowing of the channels between swamps as traps in which to place netted bags. In his diary Wells records:

Just now [July] there is fish to be had out of the swamps, and we got one of the native females to make us a net. They are made of a long kind of soapy platt [sic.], but flat and round, quite as large as an umbrella top. It is then doubled not unlike a huge ankle boot, and at the two ends there is a small opening. It is then raised from the bottom in such a way that the fish when

³⁰ The South Australian Museum has a bark canoe (A6443) from Avoca Station on the Darling River that contains an early 20th century mock-up made by museum artisans of the fireplace for display. The original fireplace was made in a mud-lined wooden container (A53554).

³¹ Jacob Harris, an Aboriginal man at Point McLeay writing in 1894, claimed that the use of the 'rude kind of raft' made from reeds predated the use of bark canoes in the Lower Murray (J. Harris letters, D6510(L) 14,15, Mortlock Library, Adelaide). The South Australian Museum holds raft specimens (A14632, A14633) made by a Yaraldi woman, Amy Johnson, in 1930.

³² This statement derived from accounts by Meintangk woman, Ethel Watson, and Tangani man, Clarence Long (Milerum) (Tindale 1931–34: 69, 87).

caught cannot return. The net is then fastened with sticks in a narrow channel where one swamp runs into another and all fish going with the stream are caught. These fish the blacks call Coogolthee. The nets are laid overnight and by break of day next morning we have plenty brought us for breakfast.³³

On the frontier of British colonisation, wild foods and Aboriginal labour were often crucial to the survival of European settlers (Clarke 1996). Examples of more active manipulation of the environment were the construction of long trenches by Aboriginal people to concentrate fish, in the long term saving them much labour expenditure. For instance, Smith records that in the Murray region:

In the low-lying country, alongside of the river, trenches are dug two or three hundred yards [180 or 270 metres] long and from four to five feet [1.2 to 1.6 metres] deep. When the Murray becomes flooded it overflows its banks to the extent of a mile or more [1.6 kilometres or more] on each side, and frequently the Murray cod, the bream, the butterfish, and other fish are living in this water. When the waters become low through evaporation and soakage the fish are easily caught ... They wade into the shallow water and scoop the fish into baskets made especially for this purpose (Smith 1930: 229).

These channels were often relatively large modifications of the landscape that would have had a significant impact upon the local watertable (Lourandos 1997: 219–22).

Another modification of the landscape for fishing was the building of stone and wooden fish-traps. Some fish-traps, probably the predominantly wooden ones, were known by the Ngarrindjeri name, *ku:yitaypari*.³⁴ The Yarlaldi people in the Lower Lakes did not make such structures, preferring to use fishing spears instead (Tindale 1931–34: 73–75). In the Coorong fish were harder to spear due to the prolific waterweed, so the Tangani relied heavily upon stone fish-traps, *talaipar* (Tindale 1931–34: 73–75). Areas of shallow water in the Coorong, such as at the Yungurumbar crossing place, were

considered good places for making such stone fish-traps (Tindale 1931–34: 71).³⁵ The Tangani generally placed their fish-traps made from limestone blocks along the landward shore of the Coorong (Tindale 1974: 61–62). This was presumably because the water here is shallow and covers a limestone shelf, in contrast to the seaward side of the Coorong lagoon, which is deep and sandy. Tindale provided a detailed record of the construction and use of fish-traps or, as his informants called them, ‘fishing-stations’ (Tindale 1931–34: 73–75, 1934–37: 5). The fish-traps were generally made in the shape of a V, with one of the walls, termed *nganangkure* or *ngalde*, connecting with the bank. The wall that extended into the Coorong lagoon was sometimes up to 30 metres long. The basketware trap was placed at a gap in the base of the V. The species of fish seasonally caught in the traps included *kongoldi* (probably congolli), *njindumi* (an eel species), *palengoi* (unknown species), *lapalap* and *therugarai* (unknown fishes, not found in the Lower Lakes) and *teri pateri* (‘sand mullet’) (Tindale 1931–34: 75, 1934–37: 5).³⁶ No attempt was made to drive the fish in, relying solely on their natural movements.

At Noonamena, on the mainland side of the Coorong near Meningie, the tops of silted over fish-trap formations can still be seen. Aboriginal people interviewed by the present author in the early 1980s said that these fish-traps were naturally formed stone structures that were previously modified and maintained with stones and pieces of wood. According to Ngarrindjeri man Jack Koolmatie, mullet travel northwards up the Coorong during the day (Ely 1980). Upon reaching the trap, fish would swim into the wide mouth of a horseshoe-shaped line of rocks. The foundation of this was a natural reef of exposed rock with all gaps except one narrow exit shored up with logs and boulders. The mullet were forced to travel through this narrow exit where a net or basketry container put in their path would catch them.

Elsewhere in southern Australia, some of the fish-traps have been described in the literature as

³³ Wells, 16 July 1853. The species of fish referred to here is probably *kungali* (congolli, *Pseudaphritis urvilli*) (Clarke 2001b).

³⁴ Yallop & Grimwade (1975: 55) list *ku:yiti* as ‘rushes, sticks’, and *ku:yitaypari* as ‘fish-trap, barrier of sticks’.

³⁵ The Yungurumbar crossing place is probably that between Rabbit Island and Junggurungbar (pronounced Yunggurungbar), a hill on the Younghusband Peninsula (see Tindale 1938, fig.1).

³⁶ The eel species referred to here is probably *Anguilla australis*. The *palengoi* was said by Tindale to be equivalent to the Yarlaldi *pelingi*. This is probably the *pelanggi* that Berndt & Berndt (1993: 308) described as ‘mudfish’ or ‘butterfish’. The *lapalap* may possibly have been a species of *Galaxias*. In the case of *teri pateri* or ‘sand mullet’, Tindale (1931–34: 74) said that its Yarlaldi name is *weialapi*. This is probably the same word as the ‘welappi’ or ‘mullet’ recorded by Taplin (1879: 131). Eckert & Robinson (1990: 19) consider that this refers to the ‘jumping mullet’ (*Liza argentea*).

weirs.³⁷ According to Edward J. Eyre, Aboriginal people seasonally gathered at the channels around Moorundie that connected the river flats with the Murray River:

making a weir across them with stakes and grass interwoven, [would] leave only one or two small openings for the stream to pass through. To these they attach bag nets, which receive all the fish that attempt to re-enter the river. The number procured in this way in a few hours is incredible. Large bodies of natives depend upon these weirs for their sole subsistence, for some time after the waters have commenced to recede (Eyre 1845, 2: 253).

This practice occurred during early December when the Murray River floods had already reached their highest point and were beginning to recede. Further south, in the shallow waters and swamps of Lake Frome near Burr Range, small fish were caught in weirs (Angas 1847b: 174). Also in the South East, near Rivoli Bay, Angas recorded:

On some of the swamps the natives had built weirs of mud, like a dam wall, extending across from side to side, for the purpose of taking the very small mucilaginous fishes that abound in the water when these swamps are flooded (Angas 1847b: 155).

In the pre-European period, Aboriginal modification of the riverine landscape for fishing must have been considerable. It was oral history among old river boat captains in the 1980s that before the lock system was introduced, remains of Aboriginal built fish-traps were known hazards to paddle-steamers when the water level was low (T. Sim, pers. comm.). Hahn recorded that in the Hahndorf area of the Mount Lofty Ranges, the Aboriginal people would:

build a dam into the river, high enough to let about a foot [31 centimetres] of water stream over it. Because of this dam, the fish in their run must come close to the surface of the water, where the savages stand in readiness to spear them (Hahn 1838–39 [1964: 133]).

In coastal zones weirs of brushwood constructed at mouths of creeks caught fish left by receding tides (Angas 1847b: 112). Some of the trenches, traps and weirs were designed to catch bait for much larger fish. For example, near Martin Well on the Coorong, drains 100 m in length were constructed by Aboriginal people to catch small fish, called *lap-lap*, for bait (Worsnop 1897: 106).³⁸ These were netted in fine close mesh nets. These weir and trench constructions appear similar in design to the much larger earthworks at Lake Condah in western Victoria.³⁹

Outside the Lower Murray, but elsewhere in southern South Australia, fish-traps have been recorded in the Port Lincoln estuarine area (Martin 1988; Mountford 1939), as well as at the mouth of Pedlar Creek south of Adelaide (Stapleton & Mountford, no date). In the case of the latter, the Tangani man, Milerum, knew of these traps as he and his family camped there, when he was a child, on their way to Adelaide via the coast.⁴⁰ There were also fish-traps made from large water-worn boulders at Moana Cove, also south of Adelaide, but these were in poor condition when Tindale inspected them in the 1920s.⁴¹ Some traps could be dragged out of the water when fish were not required. For instance, Charles Sturt stated that on his 1830 expedition down the Murray River he:

observed some cradles, or wicker frames, placed below high water-mark, that were each guarded by two natives, who threatened us violently as we approached. In running along the land, the stench from them plainly indicated what they were which these poor creatures were so anxiously watching (Sturt 1833, 2: 165).

Small dams or 'pounds' might not only be structures for catching fish, but were also used to keep part of the catch alive for future use. At the Point McLeay Aboriginal Mission, 'fish pounds' made of stakes were in common use by Aboriginal people during George Taplin's period there (1859–79).⁴² According to Lower Murray man

³⁷ For example, Beveridge (1883: 48); Curr (1883: 110) and Pretty et al (1983: 119). Tindale listed 'fish weir (set in creek)' as *ake* in a Murray River dialect (Tindale, 'Ngaiawung vocabulary', Archives, South Australian Museum, Adelaide).

³⁸ This fish, *lap-lap*, was possibly a species of *Galaxias*. *Lapps Lapps* was recorded to mean 'small fish' in the Booandik language (Smith 1880: 3). Wells (1852–55) listed *lap-lap* as 'very small fish'. Tindale (1931–34: 74) said that *lapalap* were a Coorong fish species not known in the Lower Lakes.

³⁹ For a description of the Lake Condah eel-traps, see Coutts et al (1978); Flood (1995: 240–245; 1999: 216–220); Hemming (1985); Robson (1986) and Worsnop (1897: 104–106). The S.A. Museum has a basketry trap, A6431, collected from Lake Condah, c.1910 (see figure in Hemming & Jones 2000: 9).

⁴⁰ Tindale (no date, 'Milerum', Stage A, #3, Archives, South Australian Museum, Adelaide).

⁴¹ Tindale (no date, 'Milerum', Stage A, #1, Archives, South Australian Museum, Adelaide).

⁴² The 'fish pounds' were recorded by Taplin on the shore of Lake Alexandrina (Journals, 11–12 October 1859; 8 November 1859; 11 November 1859; 28 November 1859; 10 January 1860; 21 November 1861; 20 March 1862).

Lindsay Wilson, interviewed by the present author in the early 1990s, the practice of fish storage in wooden enclosures in the lake at Point McLeay continued until the 1930s. During the early twentieth century along the Coorong, European fishermen kept alive the bream they had caught by putting them in 'pounds' made of tea-tree stakes, until the weather was suitable for transporting them to the market (Evans 1991: 40).

CULTURAL ASPECTS

Aboriginal people along the Murray River considered that their Dreaming Ancestors created the wetlands that provided them with abundant sources of food. For instance, Natone, an Aboriginal man from the South Australian section of the Murray River, claimed that a blind woman, Noreela, had created the environs of the river (Bellchambers 1931: 112, 125). Starting from Lake Victoria, Noreela, with two young children to guide her, made the river by driving back the sea. She travelled like a 'drunken bee'; her meandering course meant that the river was very long. This lengthening of her journey was considered greatly desirable, as it increased the number of fishing and hunting grounds, with a lagoon at each elbow. The fossils jutting out of cliffs along the Murray River were said by Aboriginal people to be the remains of fish killed and eaten by Noreela and her children. Another account, still told by Ngarrindjeri people in the 1980s, was of a Thukabi Ancestor, who was a large river turtle that came down the Murray River:

Thukabi [a large river turtle] came down [from the Darling district] through the desert looking for a place to lay its eggs. As she went, the drag of its tail made the river, its flipper carved out the lagoons and banks. You can see where it went. When it got to the lake, it pushed itself into the sea (H. Rankine cited Clarke 1994: 114).

In all these accounts, the present course of the Murray River is explained by the actions of Ancestral Beings.⁴³

In the Ngarrindjeri Dreaming of the Lower Murray, Ngurunderi chased a large Murray cod, Pondi, down the Murray River, widening its banks in the process, until it was eventually speared near the Murray Mouth (Berndt & Berndt 1993: 224; Clarke 1995: 148–149; Hemming & Jones 2000).⁴⁴ Whilst Ngurunderi was at the Murray River entrance into Lake Alexandrina, a water spirit known as the Mulgyewonk tore holes in his nets, which prevented him fishing for his family (Tindale & Pretty 1980: 50). There are accounts of Aboriginal legends from further upstream in Murray–Darling Basin where the dreaded river spirit who fed on boys was a large Murray cod (Sinclair 2001: 120–121, 252). Ngurunderi made the fishing grounds and lookouts for the Lower Murray people, which is told in song (Tindale 1931–34: 259).

Fish species also appear elsewhere in Lower Murray mythology. For instance, Yamakawi (Shark Ancestor) had a prominent role in the Kondoli (Whale Ancestor) Dreaming of Encounter Bay, which explained the origin of fire (Clarke 2001a: 24–25). There is also a Dreaming myth relating predominantly to freshwater fishing technology, which took place in the region from Lake Hindmarsh in western Victoria to Lake Alexandrina in the Lower Murray (Harvey 1939ms, 1943; Tindale 1934–37: 65–69). In this account the drum-nets of the pelicans were transformed into large pouches under their bills. In the Dreaming of Limi (= Lime), the love of eating fish is involved in explaining the creation of the Inman and Hindmarsh Rivers of the southern Fleurieu Peninsula (Berndt & Berndt 1993: 311; Meyer 1846 [1879: 202]).⁴⁵ The Skyworld landscape contains a fish too, with a constellation of stars being Nunganari, the Stingray (Berndt & Berndt 1993: 164, fig. 25; Clarke 1997: 131).⁴⁶

Economically important fish species were considered by the Lower Murray people to have been created by Ancestors during the creation period. For instance, in a Ramindjeri account of the Kondole (Whale) Dreaming, the Kuratje and Kanmari Ancestors became small fish when they ran in the sea:

⁴³ From the late 1980s, an animated version of this myth was given at the Signal Point Museum, Goolwa.

⁴⁴ Sinclair (2001: 120) speculated that the relatively large size that some cod grow to, up to 1.8 metres, enhanced Aboriginal beliefs of the beast's mythical qualities.

⁴⁵ Berndt & Berndt (1993: 311) suggested that Limi was a Stingray or Carpet Shark Ancestor. Meyer (1843 part 2: 75) listed 'Lime' as a 'kind of seal'. Limi and his family were eventually transformed into a group of prominent rocks in the sea at Victor Harbor near the Bluff (Meyer 1846 [1879: 202]).

⁴⁶ According to Tindale (no date, 'Milerum', Stage A, #1, Archives, South Australian Museum, Adelaide), the Tangani considered that there were seven stars shaped like a stingray.

The latter was dressed in a good kangaroo skin, and the former only a mat made of seaweed, which is the reason, they say, that the kanmari [mullet, *Aldrichetta forsteri*] contains a great deal of oil under the skin, while the kuratje [Western Australian salmon, *Arripis truttaceus*] is dry and without fat (Meyer 1846 [1879: 203]).⁴⁷

In other Dreaming accounts, the Murray cod, Pondi, was cut into smaller pieces by either Ngurunderi or Waiyungari, depending on the myth version, and thrown back into the water to become different types of fish (Clarke 1995: 148; 1999b: 53–54).

The Ramindjeri version of the Ngurunderi myth epic, recorded from Reuben Walker in 1935, starts from a large lake near mountains somewhere to the northeast of the Lower Murray and involves a large fish which is not a Murray cod:

Ngurunderi came to the Lake and speared the fish which, made off with it at a great speed and cut a deep track right down to Lake Alexandrina. Ngurunderi followed and noticed that the river thus formed was without fish. So he stood on the bank and broke the bark of the red gum tree (*wuri*) up into shreds & threw it into the water and said; you are Murray cod. This must be true because, when you cut open a Murray cod you can see a tree like mark of blood vessels on the walls of its body; it is just like a gumtree. Ngurunderi then threw in *pujulanki* bush (Native wild grape? *Cryptandra hispidula*) and this became catfish (*Tandanus tandanus*). He threw in peppermint gum bark (*tentumi*) and it became the *tjiri* (*Terapon bityan* Mitchell). After he had made all the best fishes he threw in a piece of refuse and it became the Bony bream (*tukari*, *Fluvialosa richardsoni* (Caselman)).⁴⁸

In relation to the blood vessels, it is worth noting that along the Murray European fishers have an analogous belief which interprets the tree-like markings on cod swim bladders as 'skin maps' that show the birth place of the individual fish (Sinclair 2001: 124–127). Tindale recorded from a European settler the following Dreaming account involving Matumeri who:

... chased a large fish from the sea entrance of the Murray Mouth up through the Lake until he caught it out off Poltallock [Poltaloch Station] where he killed it and pulled it to pieces and threw the pieces all about and they turned into small fishes and that is how the different sorts of

fish came (RD Anderson 1934 [cited in Tindale 1934–37: 175]).

The Ancestor mentioned here is probably Matamai, who was Ngurunderi's son (Clarke 1995: 146). The theme of an Ancestor tearing up large beings to make many smaller species also occurs in relation to kangaroos according to one account of the Waiyungari mythology (Clarke 1999b: 54).

Aboriginal people considered themselves as having a role in the continuation and wellbeing of their environmental resources. Ceremonies were sometimes performed in order to increase fish supply. For instance, Howitt relates:

There is a spot at Lake Victoria [= Lake Alexandrina], in the Narrinyeri [= Ngarrindjeri] country, where when the water is, at long intervals, exceptionally low, it causes a tree-stump to become visible. This is in charge of a family, and it is the duty of one of the men to anoint it with grease and red ochre. The reason for this is that they believe that if it is not done the lake would dry up and the supply of fish be lessened. This duty is hereditary from father to son (Howitt 1904: 399–400).

The illicit involvement between Waiyungari and Nepeli's wives in the Ngarrindjeri Dreaming was perceived as the cause of poor fishing in early spring each year. The arrival of the Young Men (Orion) and the Women (Pleiades) constellations in September was considered to help turn this around (Berndt & Berndt 1993: 164; Clarke 1999b: 57). The flowering of certain plants may also have been an indication of the arrival in the Lower Murray of certain species of fish. This was the case at Marion Bay in Yorke Peninsula, where the prolific flowering of tea-trees was a sign to the Narangga people that the mullet fish were soon to come in large numbers.⁴⁹ Here, it was claimed that initiation ceremonies were held then to take advantage of this seasonally abundant food source.

The abundance of fish would have allowed for a larger Aboriginal population in the Murray Basin in comparison to the surrounding regions. The Lower Murray was particularly rich in fish resources, involving marine, estuarine and freshwater species (Eckert & Robinson 1990; Evans 1991; Glover 1983; Olsen 1991; Sim et al 2000). Angas said 'The Milmenduras subsist

⁴⁷ Identification of these fish names is given by Eckert & Robinson (1990: 19–20). Note that *kuratye* is equivalent to *kuratje*.

⁴⁸ Tindale (1930–52: 119). [Italics by the present author.]

⁴⁹ Reminiscences recorded by E. Davies in the *Mail* newspaper, Adelaide, on 25 March 1952.

chiefly on fish, and though extremely wild and treacherous, present some of the best specimens of the Aboriginal Inhabitants, as regards physical appearance' (Angas 1847a: Plate XI). Angas also commented that 'On the S. E. coast and along the shores of the Murray and Lakes Alexandrina and Albert the natives live chiefly upon fish, and waterfowl' (Angas 1847a: General Remarks).⁵⁰ Aboriginal people considered that some of the spirits with whom they shared the landscape also liked eating fish. For example, Lower Murray people believed that the dreaded river spirit, the Mulgyewonk, was attracted to the smell of fish and once captured a young boy who was washing fish oil from his hands on the edge of the lake (Clarke 1999a: 157; Harvey 1939ms).

From the daily account available in Taplin's Journals, it is clear that fish, termed *mame* in general, were a favourite food item in the Lower Murray region. Ngarrindjeri people considered that the dominance of fish in their diet set them apart from at least some of their neighbours. They gave cultural significance to the fact that when their babies tried to speak, their first word was *mam* (Taplin Journals: 10 October 1861). Adults proudly interpreted this as the infant's desire to eat fish. The fish entrails, *ngarakuni*, were considered good eating, being grilled over the coals with the edges of the fillet curled up to catch the juices.⁵¹ Special sticks, *wunupi*, were used as fire tongs to remove food, such as fish, from hot coals.⁵² Fish remains are often found in Aboriginal middens on the banks of the Lower Lakes and Murray River (Luebbers 1978, 1981, 1982; Pretty et al 1983: 117–118; Tindale 1930–52: 67).

Some Aboriginal groups in southern South Australia were noted by their neighbours for having a diet dominated by fish. This is shown by a recorded remark by Parnkalla people of northeastern Eyre Peninsula that their Port Lincoln neighbours, the Nauo, had 'an offensive breath, being fish eaters' (Schürmann 1844, 1: 7). In the Lower Murray, Murray cod oil was rubbed on initiates (Tindale 1930–52: 139). The Tangani people of the Coorong had a song 'ridiculing men

who refused to lend their fishing net' (Tindale 1934–37: 267).

The material culture of the Lower Murray people reflected their fishing background. Old fishing nets were used in the Murray Basin for wrapping human bodies that had already been desiccated (Sheard et al 1927: 173; Tindale 1951: 258; Tindale & Mountford 1936: 495, 499). In the Lower Murray, fishing nets were often among the personal items placed in burial bundles lodged on tree platforms (Hackett 1915: 29). Stingray tail barbs or 'nails' were used in *ngildjeri* sorcery (Berndt & Berndt 1993: 260). In the Murray River area, Tindale recorded the medicinal use by Nganguruku people of Eucalyptus leaves, *tindunj*, with fish fat. Apparently they would 'infuse leaves in bark dish over hot ashes, mix with fish fat (liver) for colds'.⁵³ Angas painted an object that he described as '*Kaikoonga* – Bones of a fish found in the Murray, worn as a head ornament, in the same manner as the teeth of the kangaroo' (Angas 1847a: Plate XXX). String-games or 'cats-cradles' played by Lower Murray and South East women and children often featured 'fishing nets' (Tindale 1931–34: 88).⁵⁴

The wide distribution of recorded modifications to the landscape to assist in capturing or storing fish in the Lower Murray and neighbouring coastal and riverine areas indicates that their use, in pre-European times, was a major subsistence strategy. Lourandos has described some earthworks by Aboriginal people in temperate southern Australia as artificial drainage systems operating to flush fish from swamps into channels set with traps (Lourandos 1997: 219–221, 227). This form of swamp management coped with excess water during floods and helped retain water in times of drought. This was part of a subsistence pattern that allowed for a larger and semi-sedentary human population, in comparison to other regions. The material culture and diet of Aboriginal people living in the south would therefore have significantly differed from groups to the north and particularly those situated some distance away from major bodies of water. Fish

⁵⁰ Supporting references are Angas (1847b: Plates IX & XXV).

⁵¹ Harvey (1939ms) and Tindale (1930–52: 248–249) sketched the manner in which fish were cut up and have given the Yarlaldi names for the pieces.

⁵² Tindale & Mountford (1936: 496). See photograph in Hemming & Jones (2000: 17).

⁵³ N.B. Tindale specimens (A68579 – *Eucalyptus oleosa*; A68585 – *E. foecunda*; A75835 – unknown *Eucalyptus* species) collected '3 miles north of Swan Reach', 5 August 1964. Clarke (1989: 3) has a similar record relating to mulloway liver.

⁵⁴ In 1930 Tindale collected a string-game (A14962), called 'fishing net', from Amy Johnson (Yarlaldi people, Lower Lakes). A string-game (A66733), described as a Tangani 'fish net game' from the Coorong, was possibly a replica made by Tindale in 1934 (see Hemming & Jones 2000: 19). In 1930 D.S. Davidson and N.B. Tindale collected at Swan Reach a string-game (A14958), called a 'net', made by Jerry Mason (Yiraruka people, Murray River).

storage in pounds and mud pools was a pre-European Aboriginal practice for managing the windfall/drought situation of food gathering. Another Lower Murray technique to extend the use of fish food in pre-European times was to dry fish on racks (Berndt & Berndt 1951: 29). Because of the highly seasonal nature of fishing, it is likely that some of the stone and wood structures found in southeastern Australia, identified by archaeologists as fish or eel-traps, would be better described as fish pounds, being for storage rather than capture.

Among the Lower Murray people, many of their totemic familiars, the *ngaitji*, were species of fish (Berndt & Berndt 1993: 306–312). This was also the case for totemic groups along the Murray River (Tindale 1953: 37, 49). In their daily life, menstruating women in the Lower Lakes and Murray River areas were forbidden to eat fish (Berndt & Berndt 1993: 124–126, 141; Eyre 1845, 2: 295; Harvey 1939ms). These women were not allowed to go near the water at all, as it was considered that the success of men fishing would be spoiled. On one occasion in the past, a large incursion of seawater brought a considerable number of *poronti* (sea mullet, *Mugil cephalus*) into the Coorong lagoon (Tindale 1931–34: 119). In spite of their abundance, amongst the Tangani people only old men were allowed to eat them. The mullet would swim into the Coorong lagoon to spawn under the limestone cliffs (Tindale 1931–34: 119). In this condition only old men were allowed to spear them. Similarly, if young men ate *pelengeri* fish (unknown species), they would prematurely become baldheaded and grey (Tindale 1934–37: 39).

In the Lower Lakes no Yaraldi women, except the elderly, were allowed to eat catfish (Harvey 1939ms). Similarly, young Yaraldi girls were not allowed to eat big-bodied *kai:kuanggi* ('freshwater bream' – possibly black bream, *Acanthopagrus butcheri*). Women during menstruation were not allowed to go near water or to eat fish caught with nets, as the Yaraldi believed it would drive the fish away. In recorded versions of the Ngurunderi Dreaming, his fleeing wives cooked and ate *tukkeri* (bony bream) fish.⁵⁵ The importance of this particular episode is explained in various ways, depending on the particular account. These are that the wives were

breaking a food prohibition by eating this fish species; that the fat exploded in the fish, making them sacred to Ngurunderi; and that the wives incurred Ngurunderi's wrath by giving him the smaller of the two fish they had cooked. The unifying theme in all versions is that this fish was not to be eaten by women.

In the Murray River region more restrictions were placed upon females until past the age of child bearing than upon males of the same age (Eyre 1845, 2: 293). Teichelmann stated that in southern South Australia, food prohibitions were such that women with children were prohibited from eating certain food and that they generally lived upon vegetables (Teichelmann 1841: 7). The categories of people with least amount of food prohibitions appear to have been infants and the elderly. Eyre said that in the Murray River area 'No restrictions are placed upon very small children of either sex, a portion being given to them of whatever food their parents may have. About nine or ten years appears to be the age at which limitations commence' (Eyre 1845, 2: 293–295). He also stated that old men and women were able to eat most things. All prohibitions would have been based on cultural logic, even if the reasons were obscured from those practising the ritual. People generally excluded from prohibitions were those not sexually or economically active. It was the power to produce, either physically or spiritually, at particular life stages that was perceived as making people sensitive to influences potentially harmful to group harmony. In a sense, an individual's position in the society could be defined by what the person could eat and what economic activities they could engage in. The major categories determining prohibitions appear to have been age, gender and initiation status.

Aboriginal people could, at certain times, exercise a degree of choice in the food they lived on. For instance, some Lower Murray animal foods such as fish, emu and kangaroo meat were highly favoured foods when available. Yet vegetable foods such as roots were probably the mainstay when meat was not easily obtainable (Clarke 1988: 73–74). A report from the Adelaide-based Statistical Society in 1842 illustrates the seasonality of Aboriginal food in the southern areas.⁵⁶ The report notes that in

⁵⁵ Accounts summarised from Berndt & Berndt (1993: 224, 435), Clarke (1995: 149, 1999b: 54) and Tindale (1934–37: 285).

⁵⁶ 'Transactions of the Statistical Society. Report on the Aborigines of South Australia.' *Register* newspaper, 8 January 1842. Thomson (1939) also considered the seasonal aspects of Aboriginal culture.

spring mainly vegetables and grubs were eaten. With the commencement of summer, fish were obtained, as were kangaroos, emus, lizards and the eggs and young of birds. During the hottest part of the year possums and acacia gum were procured, while in autumn berries and nectar were available. In the winter a variety of roots were consumed, as were possums and other animals.

The coastal zones of southern South Australia were rich in natural resources, particularly food such as fish, molluscs and coastal berries. Meat from occasional whale strandings was also an attractive coastal food source (Clarke 2001a). Although many of these foods were available for the greater part of the year, the onset of winter made the coast a harsh zone in which to live. Partly for this reason, 'salt water' Aboriginal groups in southern South Australia would have moved according to season between inland and the coast. Stable isotope analysis of human bone indicates that 'salt water' groups did not penetrate up the Murray River beyond the boundaries of the Lower Murray cultural region (Pate 1997, 1998, 2000). The pattern in the Adelaide region was a general movement away from the coast in late autumn, so that more substantial shelters could be built in the protected Mount Lofty Ranges foothills (Clarke 1991: 58–59; Ellis 1976: 116–117; Ross 1984: 5; Tindale 1974: 60–61). The historical record shows similar early patterns for coastal groups from the Lower South East of South Australia (Foster 1983: 23–43). Seasonal movements, although an aspect of the Aboriginal relationship to the physical environment, are essentially dictated by the 'cultural landscape'.

A seasonal population movement occurred among at least some Lower Murray Aboriginal groups. In winter the 'salt water' Tangani people camped along the mainland side of the Coorong lagoon, where firewood was plentiful and shelter from weather available.⁵⁷ The fish-traps maintained there, where the water is shallow, provided a reliable source of food. During summer these Tangani people camped on the Younghusband Peninsula between the Coorong and the Southern Ocean, giving them easy access to coastal foods such as marine fish and berries. There were also political reasons for the movements, with the actions of neighbours impacting on Lower Murray groups. For example, one of the disadvantages of camping on the mainland side of the Coorong was that here the

Tangani were open to attack from the Ngarkat people, who normally ranged in mallee areas to the east of the Lower Murray. During harsh summers the Ngarkat people were forced towards the Murray River and Lower Lakes when their water supplies dwindled, but the Tangani considered that they were not likely to be attacked during the winter. The locations of most Lower Murray seasonal camps are not known, although more archaeological research may improve our present knowledge. For 'fresh water' Lower Murray people, such as the Yaraldi-speaking groups living along the edge of Lake Albert and Lake Alexandrina, the yearly movement was probably from the lakeshore to nearby inland areas, in order to maximise food supplies and comfort (see Fig. 2). During warmer months lakeside camps were cooler as well as being close to freshwater food sources. In contrast, during winter, campsites in close proximity to large bodies of water were more exposed to cold weather. Back from the lakeside, the forests provided natural windbreaks and had more firewood and hut building materials available. The prominence of aquatic technology used by the Lower Murray people would have given them little interest in the remote and harsh inland regions.

CONCLUSION

Resource usage by early Lower Murray Aboriginal people was a function of the broader environmental and regional patterning of the landscape. Aboriginal people in the Lower Murray were not randomly dispersed over the landscape; Ngarrindjeri people were restricted to the riparian/marine areas that were consistent with their material culture. They were, among other things, regionally organised according to their perception and use of the natural resources. The Lower Murray people considered their relationship with the environment to be an active one. Not only did they physically manipulate their resources, they also considered themselves to be influenced and organised by the environment. The material culture of the Lower Murray people, although having some aspects in common with water-based subsistence cultures in the South East and the Murray River regions, was distinctive. They were largely a cultural group confined to the riparian/

⁵⁷ Tindale (1938: 21, 1974: 61–62).

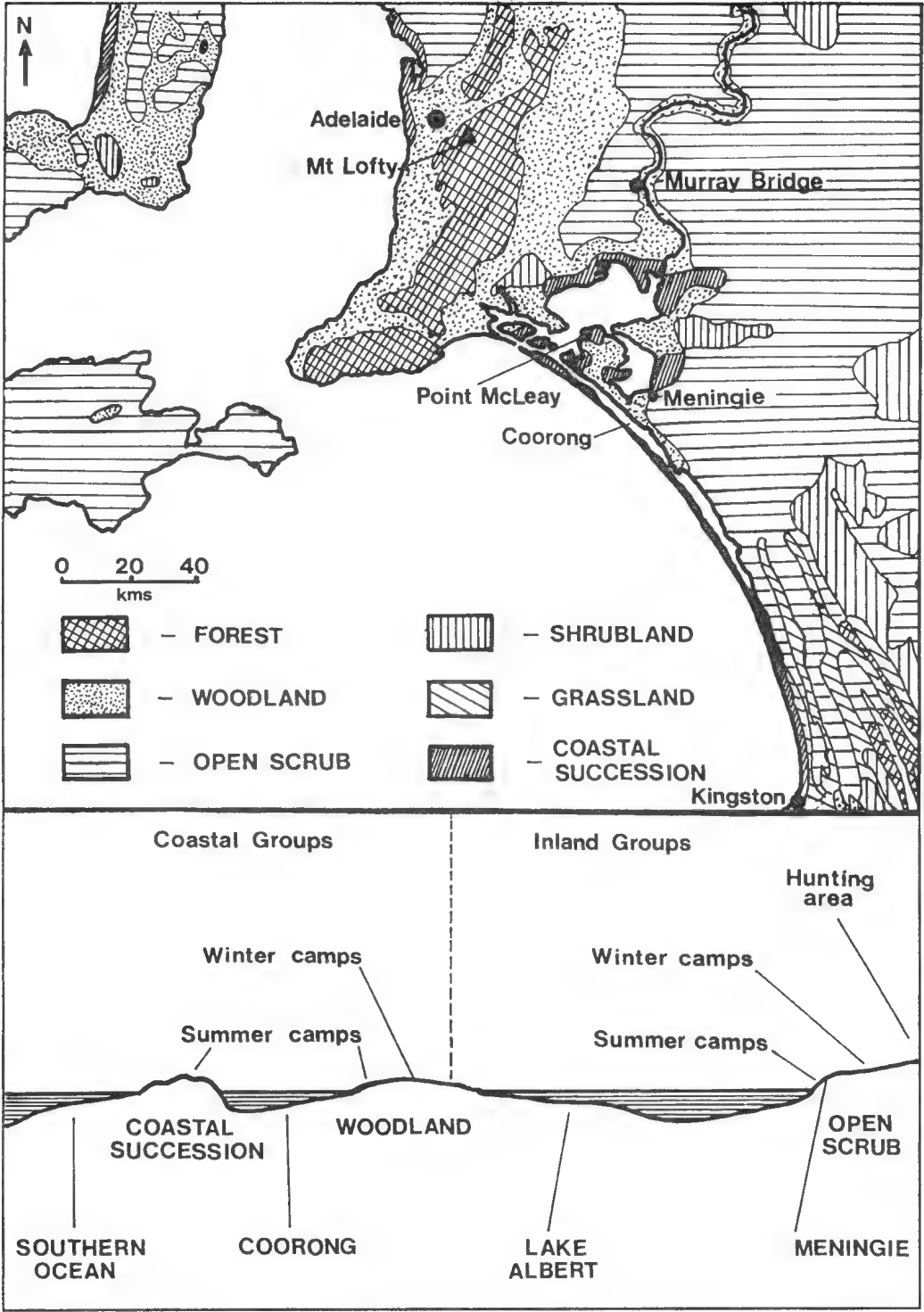


FIGURE 2. Pre-European vegetation of southern South Australia (after Boomsma & Lewis 1980: map) and Aboriginal camping zones in the Lower Murray.

coastal habitats of the southern coastal region of South Australia. Their hunting and gathering practices help to define this cultural region. Approaches in cultural geography, focusing on the cultural construction and perception of the landscape, are well suited to the study of Aboriginal environmental knowledge.

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FOSSIL LIZARDS FROM THE PLIOCENE CHINCHILLA LOCAL FAUNA, QUEENSLAND, WITH DESCRIPTION OF A NEW SPECIES

M. N. HUTCHINSON & B. S. MACKNESS

Summary

The lizard fauna of the Middle Pliocene Chinchilla Local Fauna consists of members of the Gekkonidae, Agamidae, Varanidae and Scincidae. A new species of the scincid lizard genus *Tiliqua* is described, based on a complete right dentary. The new species combines relatively unspecialised dentition, most similar to that of *T. nigrolutea*, with large size and relatively gracile proportions, with a relatively slender coronoid process and deeply concave margin between the coronoid and angular processes. An additional scincid dentary is probably referable to the genus *Cyclodomorphus*. Cranial remains of a species of the gekkonid genus *Diplodactylis* are described, representing a group of species within *Diplodactylus* that have a vestigial jugal. An agamid dentary and two varanids of differing sizes are also described.

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The lizard fauna of the Middle Pliocene Chinchilla Local Fauna consists of members of the Gekkonidae, Agamidae, Varanidae and Scincidae. A new species of the scincid lizard genus *Tiliqua* is described, based on a complete right dentary. The new species combines relatively unspecialised dentition, most similar to that of *T. nigrolutea*, with large size and relatively gracile proportions, with a relatively slender coronoid process and deeply concave margin between the coronoid and angular processes. An additional scincid dentary is probably referable to the genus *Cyclodomorphus*. Cranial remains of a species of the gekkonid genus *Diplodactylus* are described, representing a group of species within *Diplodactylus* that have a vestigial jugal. An agamid dentary and two varanids of differing sizes are also described.

Mark N Hutchinson, Department of Herpetology, South Australian Museum, North Terrace, Adelaide, South Australia 5000. Brian S Mackness*, School of Biological Sciences, University of New South Wales, Kensington, New South Wales 2052. *Current address: PO Box 560, Beerwah, Queensland 4519, Australia. Manuscript received 17 April 2002.

The Chinchilla Sand was named by Woods (1960) for a sequence of weakly consolidated grey to yellowish and light brown sands, ferruginised heterogeneous conglomerates, grits, sandy clay and clays. These outcrops range from shallow beds to sections several metres deep along a 40 km stretch of the Condamine River valley, approximately 240 km ENE of Brisbane.

The Chinchilla Sand has yielded a diverse array of fossil remains, the Chinchilla Local Fauna (Mackness, Wilkinson & Wilkinson 1999). Mammals have been the best studied group and the fauna recovered comprises macropodids (Bartholomai 1963, 1966, 1967, 1973, 1975, 1976; Flannery & Archer 1983), phascolarctids (Archer 1977), thylacoleonids (Archer & Dawson 1982; Bartholomai 1962; Woods 1956), peramelids (Mackness et al 2000), dasyurids (Archer 1982; Bartholomai 1971; Dawson 1982; Wroe & Mackness 1998, 2000a, 2000b), a thylacine (Mackness et al submitted), murid rodents (Godthelp 1990) and a molossid bat (Hand et al 1999). At least three lineages of birds are also known, an emu, a rail and a duck (Olson 1975, 1977; Patterson & Rich 1987). The living lungfish *Neoceratodus* and plotosid catfish have also been recorded (Kemp & Molnar 1981; Mackness et al 1999). Reptile remains described so far pertain to larger taxa, such as crocodilians

(*Palimnarchus*), turtles and madtsoiid snakes (Bartholomai & Woods 1976; Gaffney 1981; Gaffney & Bartholomai 1979; Mackness & Scanlon 1998; Woods 1960, 1962). The only lizards to date have been Hecht's (1975) identification of a number of large varanid fossils from the Chinchilla Local Fauna as *Megalanina* sp.

The Chinchilla Local Fauna appears to biocorrelate with the Kanunka Local Fauna of the Tirari Desert, South Australia (Tedford et al 1992) and the Spring Park, Bow and Big Sink Local Faunas (Mackness et al 2000). On the basis of the Kanunka Local Fauna having a magnetostratigraphic age of approximately 3.4 million years, the Chinchilla Local Fauna is estimated to be between late Early Pliocene and Middle Pliocene in age (Tedford et al 1992).

Lizard fossil remains have received relatively little attention in reports on Australian fossil faunas, due both to a paucity of material and a lack of data concerning osteology. In some lineages of lizards, such as agamids (Covacevich et al 1990) and varanids (Mackness & Hutchinson 2000), the restricted amount of morphological divergence within the living fauna makes identification problematic. For the anatomically diverse skinks and gekkonoids, this picture is steadily changing for the better as new finds focus attention on specific areas of anatomy. In this

study we point out some useful character states of gekkonid skulls that permit attribution to both major lineages and more restricted species groups. We also build on the knowledge of one of Australia's most characteristic lizard faunal elements, the bluetongue skinks of the genus *Tiliqua* (Shea & Hutchinson 1992) to describe a new and distinctive species.

MATERIALS AND METHODS

The specimens described here were recovered through quarrying or wet sieving of sediments from 'Wilkinson's Quarry', Chinchilla, Queensland, a site that has been continuously worked by Cec and Doris Wilkinson for over 11 years. The sediments are primarily fluvial in nature and represent a number of depositional events. Most fossils in these units occur as isolated pieces and all represent Pliocene taxa (Mackness, Wilkinson & Wilkinson 1999).

Specimens were examined using a Wild M3Z stereomicroscope with eyepiece micrometer and drawing tube. The fossils are registered in the collection of the Queensland Museum, Brisbane and were compared with skeletal material in the collection of the South Australian and Western Australian Museums. Comparative scincid specimens included all living species of *Tiliqua* and representatives from all species groups in the genera *Cyclodomorphus* and *Egernia*. The morphology of the gekkonid fossils dictated the gekkonid specimens that would be the most likely candidates for comparison, the 'unspecialised' small- to medium-sized diplodactylines. We also examined representatives of those genera of gekkonines that occur in the Australian region and the adjacent Melanesian-Indonesian region, as well as a scattering of specimens from across the global diversity of the subfamily Gekkoninae. In addition, published diagrams and discussions of gekkonid cranial osteology were consulted to ensure that our selection was representative, mainly aimed at justifying some of the general statements we make regarding major patterns of variation that differentiate gekkonine and diplodactyline skulls and mandibles. Specimens examined are listed in Appendix 1. Terminology for bones follows Estes et al (1988).

Measurements

Measurements of varanid vertebrae and the large *Tiliqua* species were made using Vernier callipers accurate to 0.05 mm, while smaller

specimens and teeth were measured with a calibrated microscope eyepiece. Vertebral measurements are summarised below and largely follow Smith (1976). Statistical analyses of these measurements are provided in Appendix 2; Tables 1 and 2.

Vertebral length (Pr-Po) — the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis.

Vertebral width (Pr-Pr) — the maximum width of the vertebra between the lateral edges of the prezygapophyses.

Vertebral width (Po-Po) — the maximum width of the vertebra between the lateral edges of the postzygapophyses.

Centrum minimum width (BW) — the smallest distance across the centrum.

Condylar width (CW) — the greatest transverse diameter of the condyle.

Abbreviation for specimen numbers: AR: University of New South Wales Research Collection; SAM: South Australian Museum; WPC: Wilkinson Private Collection.

SYSTEMATICS

Order SQUAMATA Oppel, 1811

Family AGAMIDAE Gray, 1827

Unidentified material

Material examined

A left dentary (WPC 1354), bearing mid to rear section of tooth row.

Characters

Agamid reptiles are distinguished in having a dentition combining one to three anterior pleurodont teeth followed by acrodont teeth. Other agamid features are summarised by Estes (1983).

Description

The specimen is from a moderately sized individual, perhaps of skull length of approximately 30 mm, and bears nine acrodont teeth. The posterior of the dentary is largely missing although the facet for the coronoid is still visible. No mental foramina are discernible on the specimen.

Remarks

Covacevich et al (1990) discussed several problems in identifying fragmentary agamid remains beyond family level.

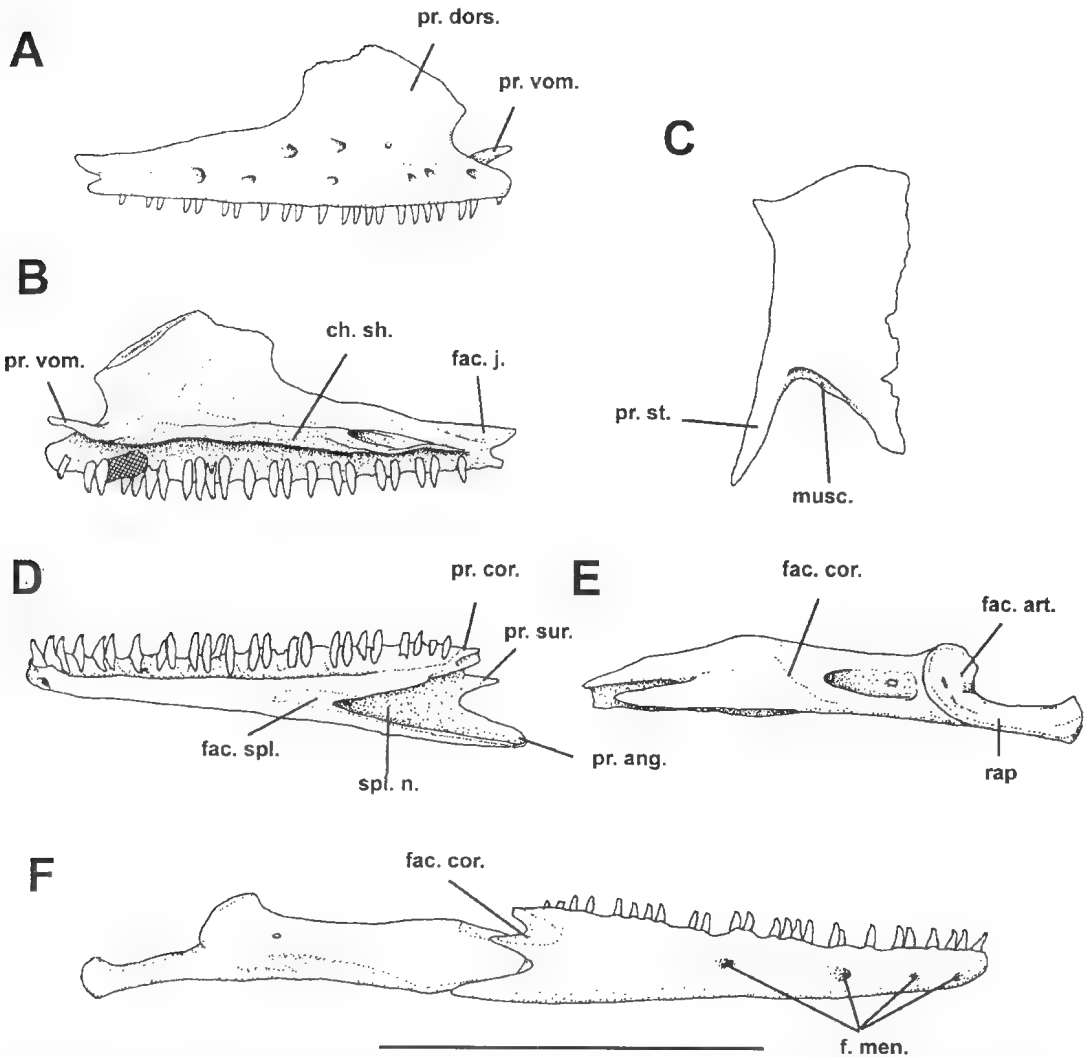


FIGURE 1. **A–F** *Diplodactylus cf steindachneri*. **A**, right maxilla (QM F30573) in lateral view and **B**, medial view. **C**, left parietal (QM F30574) in dorsal view. **D–F** right mandible (QM F30572). **D**, lingual view of dentary. **E**, lingual view of articular + surangular. **F**, articulated mandible in labial view. Abbreviations: ch. sh. – choanal shelf; f. men. – mental foramina; fac. art. – articular facet; fac. cor. – coronoid facet; fac. j. – jugal facet; fac. spl. – splenial facet; musc. – insertion point for dorsal neck musculature; pr. ang. – angular process; pr. cor. – coronoid process; pr. dors. – dorsal process; pr. st. – supratemporal process; pr. sur. – surangular process; pr. vom. – vomerine process; rap – retroarticular process; spl. n. – splenial notch. Scale bar = 5 mm.

Family GEKKONIDAE Gray, 1825

Subfamily DIPLODACTYLINAE Underwood, 1954

Diplodactylus Gray, 1825

Diplodactylus cf steindachneri
(Fig. 1A–F)

Material examined

Right maxilla (QM F30573); left parietal (QM F30574); partial right mandible (QM F30572), consisting of a dentary and fused surangular plus articular.

Description

Maxilla. The maxilla (QM F30573, Fig. 1A–B), a right element, is almost complete, with slight

erosion of the edges on the margin of the dorsal process. Total length 6.1 mm. A slender, dorsoventrally flattened vomerine process extends medially from the anteromedial end of the bone. The facial portion of the maxilla is gently arched along its dorsal margin. Although the dorsal margin is slightly damaged, there is no posterodorsally directed frontal process. The margin bordering the nasal opening is almost semicircular. The outer surface of the maxilla bears two series of foramina; one consisting of a row of six openings just above the teeth, the posteriormost the largest; and a second consisting of three relatively large openings at the level of the anteroventral corner of the orbit. The subocular ramus of the maxilla is robust and relatively short and deep. It does not taper to a point, as is usual in gekkonoids; the outline of the caudal extremity of the specimen is bifurcated, with the dorsal fork larger than the ventral. The internal surface of the maxilla bears a prominent choanal shelf, which is constricted at its mid-point and again anteriorly before projecting as the vomerine process. The inner face of the suborbital region has a small facet for a vestigial jugal on the dorsal fork, below which is a longer facet for the ectopterygoid.

There are 33 tooth loci, most with intact teeth. The teeth are small, cylindrical in section and tapering to acute points, with an apical cusp and lingual cusp separated by a narrow occlusal groove; this morphology is regarded as typical and plesiomorphic for gekkonoids (Sumida & Murphy 1987). The individual teeth are uniform in size and vary only slightly in shape.

Parietal. The left parietal (QM F30574) (Fig. 1C) is complete except for slight erosion along the medial margin. In common with many living species, the medial edge of the bone may not have been fully ossified. Beginning at the bone's anteromedial apex, the anterior margin describes a shallow sinusoidal curve posterolaterally, terminating at the obtusely pointed apex of the articulation point with the postorbital. The caudal margin of the body of the parietal is almost straight-edged and faces caudolaterally. This margin bears a shallow caudally opening pocket, which would have been the insertion point for the superficial neck musculature. The supratemporal process is relatively slender and tapers to an acute point. Ventrally, the bone bears a descending flange parallel to the lateral margin, the flange descending to a pointed projection (epipterygoid process) about halfway along. Overall length of the specimen is 4.2 mm;

width (measured at the apex of the postorbital articulation) 1.9 mm.

Adult mandible (QM F30572, Fig. 1D–F) is represented by a complete dentary and nearly complete compound bone consisting of the fused articular and surangular bones. The angular, splenial (or the composite angulosplenial typical of diplodactylines) and coronoid are absent.

Dentary. Total length (taken as a straight line from symphysis to tip of angular process) 6.5 mm. There are 36 teeth or tooth loci, the teeth being similar in size and shape to those on the maxilla, with the most anterior teeth having somewhat more recurved tips.

The dental sulcus is well defined by a lingual parapet that is evident as far as the posteriormost tooth. The posterior limit of the bone has three processes, which define two embayments. The uppermost (coronoid) process terminates just behind the last tooth and has facets on its lingual and labial aspects for the coronoid bone. The middle (surangular) and lower (angular) processes would have terminated at about the level of the apex of the dorsal process of the coronoid bone. The labial face bears four mental foramina, the posteriormost lying at the level of the 24th tooth. On the lingual face, the splenial notch extends forward to the level of the 27th tooth, and there is a facet extending anteriorly to the notch, suggesting that the splenial terminated at about the level of the 22nd tooth. There is no bony intramandibular septum exposed within the splenial notch.

Comparisons

The identification of these specimens as gekkonoids is based on several characters that are uniquely combined in this clade. The morphology of the articular and retroarticular region of the mandible shows an articular facet facing posterodorsally and the retroarticular process as slender and ventrally positioned. There is complete overgrowth by the dentary of the groove for Meckel's cartilage. The teeth are small, finely pointed and numerous. The parietal is poorly ossified, paired and lacks a pineal foramen. The elements are those of a small (approx 45 mm SVL) generalised gecko.

Studies of the phylogenetic relationships among the Gekkota (Bauer 1990; Donnellan et al 1999; Estes et al 1988; Kluge 1967a, 1967b, 1987) agree that the Australian region has three of the four major gekkotan lineages: the Gekkoninae, Diplodactylinae and Pygopodidae. The remaining gekkotan clade, the Eublepharidae, is found no

closer than Borneo (the genus *Aelurascalabotes*). To further establish the affinities of the Chinchilla specimens, we have noted several characters that appear to be useful in diagnosing membership of particular gekkotan lineages, based on the most commonly recovered elements: mandibles, maxillae, frontals and parietals.

Maxilla. The shape of the maxilla differs markedly between most gekkonines and the rest of the gekkotan lineages. Authors describing this area of the face generally emphasise bony contacts, using the dichotomy of either a prefrontal–nasal contact (shown by most diplodactylines) or a frontal–maxilla contact (shown by most gekkonines) (Fig. 2). In most Australian gekkonines (*Cyrtodactylus*, *Gehyra*, *Heteronotia*, *Nactus*), and in most other gekkonines examined, the maxilla arches posteromedially to contact the frontal, terminating in a frontal process that greatly reduces the exposure of the prefrontal and excludes the prefrontal from the nasal. In the remaining Australian gekkonine *Christinus* and in

diplodactylines, the maxilla lacks this frontal process and the prefrontal includes an anteromedial process that contacts the nasal, usually excluding it from the maxilla. In eublepharids (*Aelurascalabotes* [Grismer 1988], *Hemitheconyx* [Rieppel 1984]) the prefrontals bear anteromedial processes but they are excluded from the maxilla due to well-developed anterolateral processes of the frontal; the maxilla is similar in shape to that of the diplodactylines. Pygopods are variable but most tend to show a gekkonine-like posterodorsal expansion of the maxilla to contact the frontal. The maxilla of the Chinchilla gecko has a low, gently arched dorsal process with no frontal process.

The Chinchilla fossil shows a distinctive feature of the maxilla that suggests a particular relationship within the Diplodactylinae. In lateral view its subocular ramus shows a relatively deep, bifurcate posterior termination, a characteristic also seen in a few species of the genus *Diplodactylus*. In these species the notched tip of the terminal portion of the maxilla is correlated

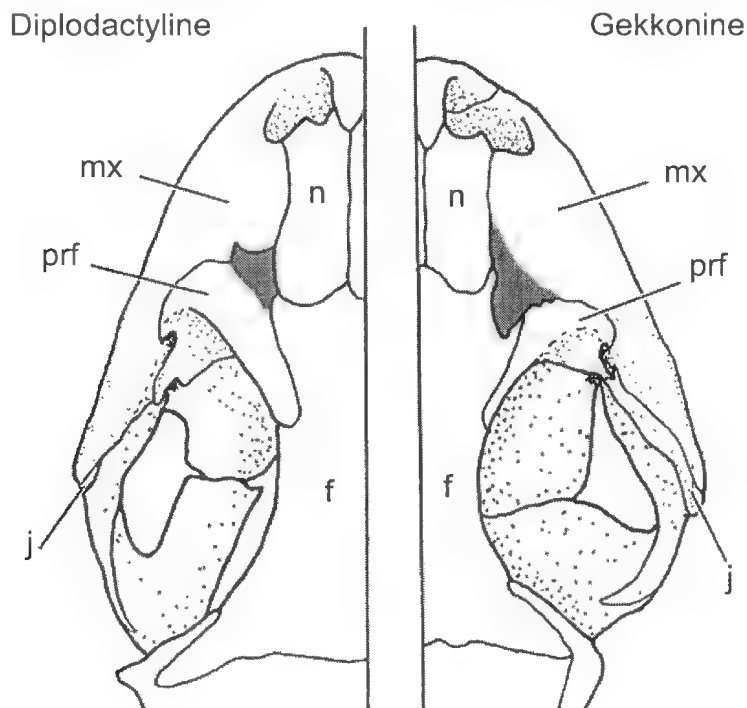


FIGURE 2. Comparison of the anterior part of the skull in a diplodactyline (*Diplodactylus stenodactylus*) and an Australian gekkonine (*Gehyra dubia*) gecko showing the usual patterns of contact between the frontal (f), nasal (n), maxilla (mx) and prefrontal (prf) bones. Areas in grey show the anteromedial (nasal) process of the prefrontal (diplodactyline), and the frontal process of the maxilla (gekkonine). *D. stenodactylus* also shows a vestigial jugal (j), compared with the usual degree of development of this bone in most other gekkotans as shown by *G. dubia*.

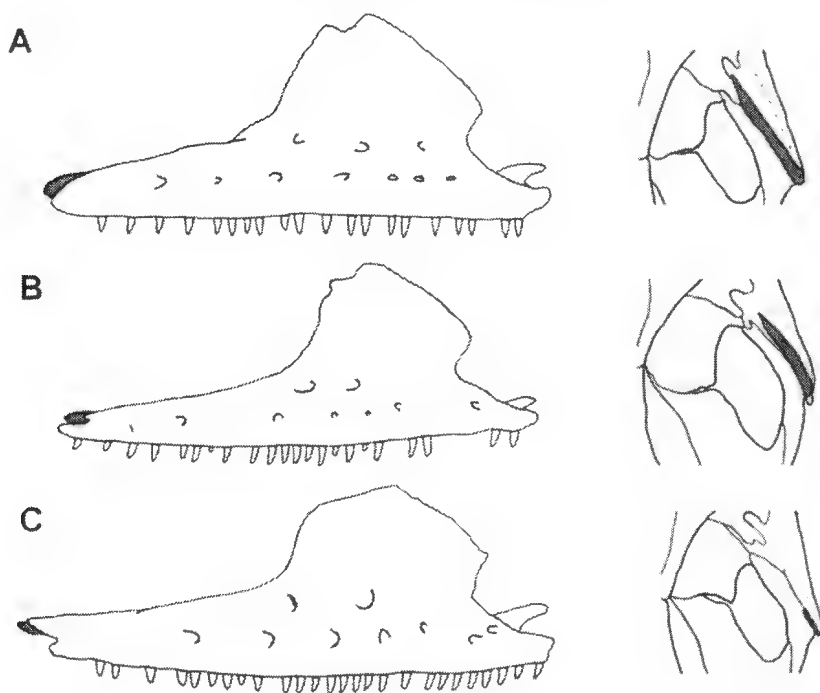


FIGURE 3. Right maxilla (slightly anterodorsal in aspect) and sketch of dorsal view of right orbit in three species of *Diplodactylus*, showing reduction of the jugal (grey). **A**, *D. granariensis* (R29135); **B**, *D. damaeus* (R24553); and **C**, *D. steindachneri* (R05153). Approx. length of maxillae 6–7 mm, not to scale.

with reduction of the jugal bone reported by Kluge (1967b). The two species reported as having the greatest reduction of the jugal (*D. steindachneri* and *D. stenodactylus*) have the most pronounced development of the bifurcate shape (Fig. 3A–C) and are essentially identical in appearance to the Chinchilla maxilla.

Frontal. No frontal has been recovered at Chinchilla, but future finds should be identifiable as gekkonine if there are three facets on its anterior portion (for the nasal, maxilla and prefrontal) or otherwise if there are only two facets. The relatively long nasal processes of eublepharid frontals might also be diagnostic for that clade.

Parietal. Many gekkotan taxa have distinctive parietal morphologies. However, this bone shows marked ontogenetic variation in its degree of ossification, the elaboration of muscle attachment points on its lateral and posterior margins, and the robustness of the supratemporal process. The most distinctive feature of the Chinchilla specimen is the concavity for the neck musculature on the posterior margin. This arrangement is not typical

of most gekkos, where the musculature simply attaches to the posterodorsal surface and edge of the parietal, or to the posteroventrally deflected trailing edge, generally with no more than a depression or a low ridge to mark the point of attachment. A more-or-less well-defined pocket is present in some members of the genus *Diplodactylus* (*D. stenodactylus*, *D. steindachneri*, *D. byrnei*, intraspecifically variable in *D. damaeus*) but is absent from other Diplodactylinae examined and was not seen in the gekkonines. Pygopod parietals are much slenderer than those of other gekkotans, the midline length being at least twice the width (cf less than 1.5 times the width).

Mandible. Some diplodactyline and gekkonine taxa as well as pygopods (Hutchinson 1997) have unique modifications of the mandible that are diagnostic for individual genera, but many gekkotan taxa have mandibles that are superficially similar in overall shape. In these generalised mandibles, the retroarticular process provides a key to the two major gecko subfamilies. In gekkonines, the retroarticular

process is generally spoon-like in shape, its dorsal surface forming an obvious, concave bowl. In most diplodactylines (*Saltuarius* and some *Strophurus* are exceptions) and in pygopodids, the retroarticular process is rod-like, with an oval, flattened or shallowly concave cross-section and terminated by a club. The morphology of the dorsal surface of the retroarticular process in eublepharids has not been described (published diagrams show only the shape in lateral or ventral view). The Chinchilla specimen has the clubbed, diplodactyline type of retroarticular process.

The fossil maxilla and mandible therefore not only show an overall similarity with diplodactylines, but also share several discrete character states that indicate specific diplodactyline affinities. The characteristics that distinguish the fossils are those that are uniquely combined in the genus *Diplodactylus*.

The Chinchilla fossils were found as disarticulated elements but their size and preservation, especially the mandible and maxilla, are consistent with having come from one animal. Based on the possession of a bifurcate terminus to

the posterior ramus of the maxilla and the presence of a 'pocket' on the trailing edge of the parietal, they are referred to *D. steindachneri*. It is one of three species of *Diplodactylus* still found in the region (the other two are *D. vittatus* and *D. tessellatus*, Ingram & Raven 1991), and is the only one of these three species to have a vestigial jugal and bifurcate maxillary terminus. The other species with reduced jugals, members of the *D. stenodactylus* group, are found in the deserts of central and western Australia, the closest to Chinchilla being *D. immaculatus* of western Queensland.

Family SCINCIDAE Gray, 1825

Subfamily LYGOSOMINAE Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua wilkinsonorum sp. nov. (Fig. 4A–B)

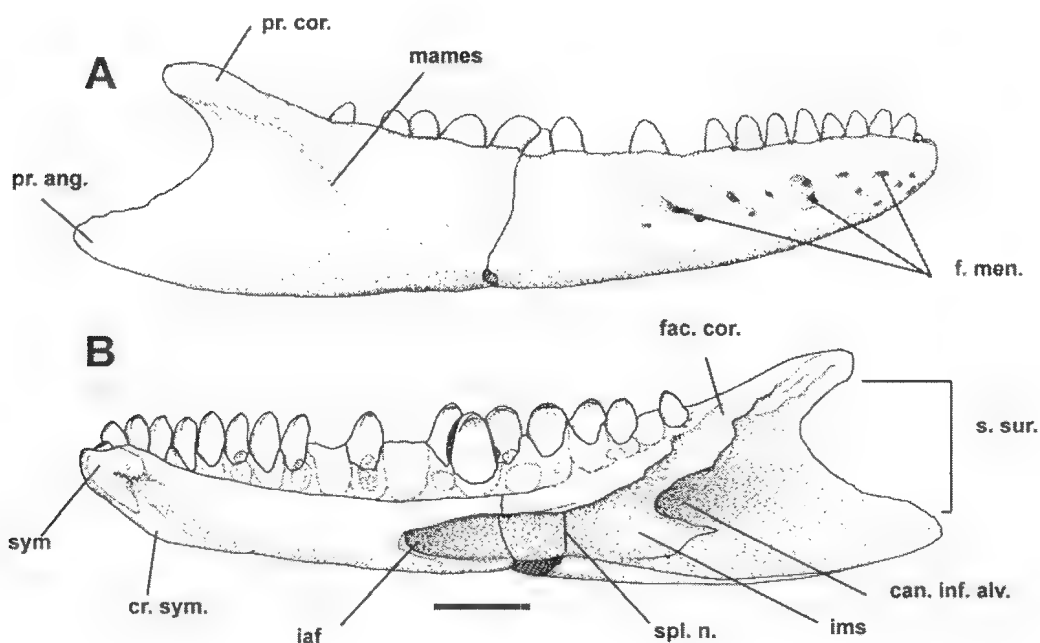


FIGURE 4. A–B *Tiliqua wilkinsonorum* n. sp. QM F30567 Holotype right dentary. A, labial; B, lingual. Abbreviations: can. inf. alv. – inferior alveolar canal; cr. sym. – symphyseal crest; f. men. – mental foramina; fac. cor. – coronoid facet; iaf – inferior alveolar foramen (= anterior inferior alveolar foramen); ims – intramandibular septum; mames – limits of attachment for external adductor musculature; pr. ang. – angular process; pr. cor. – coronoid process; spl. n. – splenial notch; s. sur. – surangular suture; sym. – symphysis. Scale bar = 5 mm.

Material examined

Holotype: a right dentary (QM F30567).

Type Locality

Wilkinson's Quarry site, Chinchilla area, southeastern Queensland. The specimen comes from a fossil-bearing unit within the quarry that lies unconformably on top of a layer of fine sand. The sediments are primarily fluvial in nature and represent a number of depositional events.

Age

Chinchilla Local Fauna, late Early to Middle Pliocene (Tedford et al 1992).

Diagnosis

A large species, dentary tooth row length 33 mm, differing from other *Tiliqua* by the following combination of characters: all tooth crowns pointed and retaining an occlusal ridge, the crown scarcely wider than the shaft; coronoid process of the dentary relatively slender, narrower than long, its shape correlated with a curved and concave, rather than angular or straight, dentary-surangular suture connecting the base of the coronoid process with the tip of the angular process.

Description

A right dentary, bearing a complete row of 20 teeth or tooth loci. The specimen is almost intact, being slightly damaged at the apex of the splenial notch and on the ventral edge adjacent to a repaired crack through the jaw at the level of the 15th tooth. Total length, from the anteriormost point of the symphysis to the tip of the angular process, 47.8 mm. Depth at level of 16th tooth (excluding tooth), 7.8 mm. Maximum depth of jaw, measured vertically from the apex of the coronoid process, 13.1 mm. Maximum width, measured in occlusal view at the level of the 16th tooth, 8.0 mm.

Meckelian groove closed, no trace of suture. A pronounced crest runs caudally from the symphysis along the ventrolingual margin of the jaw, gradually merging with the body of the dentary at about the level of the eighth tooth. Apex of the splenial notch at about the level of the 12th or 13th tooth, slight uncertainty due to the broken edge of the inferior alveolar foramen at the apex of the notch. Labial surface with pronounced, arcuate adductor muscle scar that has its apex level with the last tooth. Angular process projects 15 mm beyond the level of the last tooth. Dorsal margin of angular process merges with the

ventral margin of the coronoid process along a smooth concave curve that has its apex at the level of the tooth row. Coronoid process well developed, flattened, but relatively small compared with other *Tiliqua*. A series of mental foramina starts at the level of the 11th tooth and runs anteriorly to the symphysis. These foramina are mostly arranged as a series of superposed pairs, with a total of about nine in the series.

Intramandibular septum fused ventrally along its length to the ventral lamina of the dentary, completely separating the inferior alveolar canal from the Meckelian canal. Caudal margin of intramandibular septum with a deep, curved notch, bounded ventrally by a caudally projecting prong.

Tooth row, in occlusal view, almost straight, gently curving medially anterior to the level of the sixth tooth. Labial wall of dental sulcus tall and robust. Lingual wall low but distinct anteriorly, reducing caudally and disappearing by about the level of the 16th tooth. Lingual face of dentary below the dental sulcus vertical, sharply distinct from the tooth row. Dentition pleurodont. The first of 20 teeth is broken off and the 10th, 12th and 19th loci are empty, but all other teeth are present and well preserved. The teeth vary distinctly in size, becoming larger progressing caudally, with the maximum reached in positions 13 to 16, the subsequent teeth then diminishing in size. As a guide to the changes in tooth size, tooth 6 is 3.5 mm high by 1.3 mm wide (measured normal to the lingual aspect) while tooth 14 is 4.3 mm high by 2.4 mm wide; thus, height increases by 23% and width by 85%. In lingual view, the tooth crowns are acutely pointed anteriorly, becoming obtusely pointed by about the 13th tooth. The crown of each tooth is margined by an occlusal ridge that separates its lingual and labial surfaces. In mesial view the tooth crowns have a parabolic curved outline labially, but the lingual surface is flatter, descending almost vertically from the apical ridge and forming an angular contact with the rounded labial surface. On the largest teeth, several low striae run vertically down from the apical ridge on both labial and lingual surfaces of the crown.

Comparisons

The combination of the closed Meckelian groove, enlarged 'cheek' teeth with more than one large tooth posterior to position 10, and an enlarged and flattened coronoid process is unique and diagnostic for the bluetongue lizards of the genus *Tiliqua* (Shea 1990). The related genus

Cyclodomorphus has only a single enlarged cheek tooth, while other lygosomines with a closed Meckelian groove lack such obvious dental differentiation.

Most species of *Tiliqua*, however, have a more specialised dentition than *T. wilkinsonorum*. The plesiomorphic tooth crown morphology in skinks includes a convex outer surface, curving occlusally to a pair of apical ridges separated by a groove (M. H. pers. obs.; Sumida & Murphy 1987), while the lingual surface is flattened and oriented almost vertically, forming an angular contact with the apical ridge. In lingual and mesial views the crown is acutely pointed. In contrast to this, species of *Cyclodomorphus* and *Tiliqua* have teeth modified for durophagy (Estes & Williams 1984). Most species of *Tiliqua*, including *T. gigas*, *T. multifasciata*, *T. occipitalis*, *T. pusilla*, *T. rugosa* and *T. scincoides*, have cheek teeth with expanded crowns, and have lost or greatly reduced the plesiomorphic asymmetry of the crown. In occlusal view the crown is circular in shape, and when viewed mesiodistally the crown profile, a convex curve, is similar in shape lingually and labially. The apex of the tooth has a central conical projection with pronounced striae radiating over the crown from this central point. Most individuals lack an occlusal ridge, although many *T. occipitalis* and some *T. rugosa* have a remnant on the tooth apex. *Tiliqua adelaidensis* has quite different dentition in which the enlarged cheek teeth are labiolingually compressed, with a pronounced cutting edge formed by the apical ridge. *Tiliqua nigrolutea* is the living species that shows the closest dental similarity to *T. wilkinsonorum*. The teeth show little expansion of the crowns, which are pointed and retain an obvious occlusal ridge that demarcates the crown into lingual and labial aspects. These two species show an asymmetric tooth crown profile in mesiodistal view, with a more steeply descending lingual surface. Compared with *T. nigrolutea*, the teeth of *T. wilkinsonorum* differ only in being more robust and having the crowns of the largest teeth more expanded and obtusely pointed. These differences could be attributed to allometry or individual variation in tooth proportions, which is considerable in living *Tiliqua* (M. H. pers. obs.). However, other characteristics of the fossil specimen differentiate it from both *T. nigrolutea* and other *Tiliqua* species.

The dentary is from a very large *Tiliqua*. Using the average ratio of tooth row to mandible length (0.48) that applies in extant *Tiliqua*, the tooth row length of *T. wilkinsonorum* of 33 mm extrapolates

to an approximate mandible length of 68 mm. This size is approached only by the largest males of *T. rugosa* and *T. scincoides* (G. M. Shea pers. comm.) and suggests that *T. wilkinsonorum* may have had a snout-vent length close to 400 mm and a mass in excess of one kilogram. In spite of this size, the dentary of *T. wilkinsonorum* is notably gracile. This is most clearly seen in the shape of the coronoid process and the surangular suture running from the base of the coronoid process to the tip of the angular process. In all extant *Tiliqua*, the coronoid process is dorsally and caudally expanded. This expansion is masked to some extent because the base of the coronoid process is absorbed by caudal expansion of the trailing edge of the dentary such that the surangular suture is not deeply incised into the labial lamina of the dentary. The precise course of this suture varies both inter- and intraspecifically (Fig. 5A–I). In *T. nigrolutea*, *T. occipitalis* and *T. rugosa*, this suture usually runs vertically from the coronoid process and then angles caudoventrally to the tip of the angular process of the dentary. In *T. adelaidensis*, *T. gigas*, *T. multifasciata* and *T. scincoides*, the suture tends to run caudoventrally in an almost straight line from the base of the coronoid process. In none does it trace the excavated curve seen in *T. wilkinsonorum* (and other skinks). In *T. wilkinsonorum* the coronoid process is less expanded than in any extant species, with the possible exception of *T. gigas*, but is more clearly defined ventrally by the anterior sweep of the concave surangular suture. In living *Tiliqua* species, the expanded coronoid process and adjacent parts of the dentary increase the strength of this region of the mandible and increase the area of attachment for the jaw-closing tendon of the *m. adductor medius externus superficialis* (Haas 1973). The relative slenderness of the coronoid process and the concave surangular suture in *T. wilkinsonorum* are closer to the morphology seen in other skinks, including *Egernia*, the genus that probably includes the sister group of the *Tiliqua* lineage.

In summary, *T. wilkinsonorum* is one of the largest known specimens of *Tiliqua*, and has less specialised teeth than all but *T. nigrolutea* and a more slender (plesiomorphic) coronoid process of the dentary than all but *T. gigas*. The morphology of the teeth and the relative gracility of the caudal end of the dentary suggest that *T. wilkinsonorum* was not as specialised for durophagy as most other large *Tiliqua*.

Tiliqua wilkinsonorum is the third species of *Tiliqua* to be found in the Tertiary of Australia

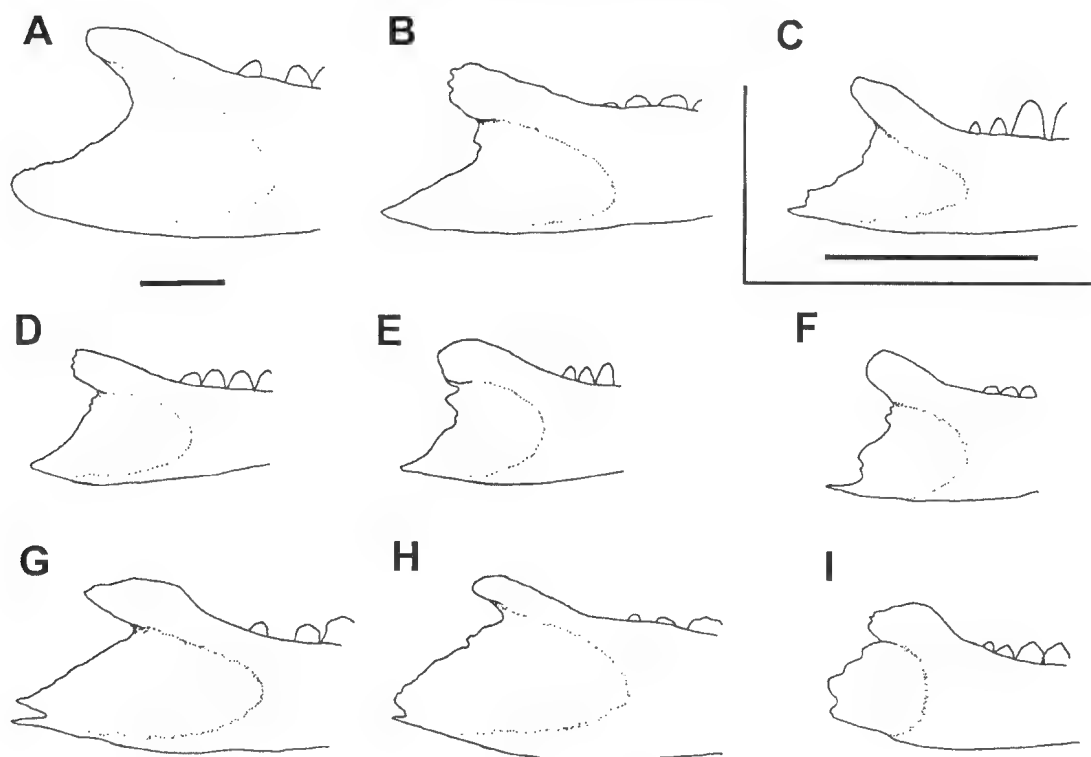


FIGURE 5. Dentary variation in *Tiliqua*. Detailed views showing variation evident in the degree of expansion of the coronoid process of the dentary and the shape of the dentary-surangular suture. All to same scale except *T. adelaidensis* (inset); both scale bars = 5 mm. A, *T. wilkinsonorum*. B, *T. rugosa* R27028. C, *T. adelaidensis* R40738. D, *T. nigrolutea* R02725. E, *T. nigrolutea* R47698. F, *T. occipitalis* R35758. G, *T. scincoides* R27039. H, *T. gigas* R11419. I, *T. multifasciata*, R35757.

and the second extinct species. Shea and Hutchinson (1992) described a very small species, *T. pusilla*, from the early Middle Miocene of Queensland, and specimens indistinguishable from a living species, *T. scincoides*, have been recorded from the Pliocene of South Australia (Pledge 1992) and Queensland (Mackness & Hutchinson 2000).

cf. *Cyclodomorphus* Fitzinger, 1843

Material examined

A partial dentary (QM F30568).

Description

The specimen represents about one-third of a left dentary, lacking the anterior portion, anterior to the last six teeth and lacking the coronoid and angular processes. It is not a juvenile, based on

several cycles of tooth replacement being evident. The groove for the Meckelian cartilage is completely obliterated by the dentary. The third-last tooth is markedly enlarged. The tooth anterior to this is absent, but its locus is smaller, while the other remaining teeth are smaller again. A single large mental foramen is present on the labial surface of the jaw at the level of the fourth-last tooth. The teeth, both enlarged and small, have blunt, slightly laterally compressed crowns with virtually no apical ornamentation such as cusps, grooves or striae.

Comparison

The fossil appears to have only one markedly enlarged cheek tooth, with a second moderately enlarged tooth anterior to it. Among extant Australian skinks, only members of the *Tiliqua* lineage combine a closed Meckelian groove and enlarged durophagous cheek teeth (Shea 1990).

The dentitions of the two genera of this lineage, *Tiliqua* and *Cyclodomorphus*, differ in that adults of *Tiliqua* have several enlarged cheek teeth while those of *Cyclodomorphus* usually have only one strongly enlarged tooth. On this basis as well as its small size and overall shape, the Chinchilla specimen is more similar to *Cyclodomorphus* than it is to *Tiliqua*. However, *Tiliqua adelaidensis* and the extinct *T. pusilla* show that the small species of *Tiliqua* may have only two enlarged cheek teeth, so that the distinction on tooth pattern alone is not entirely conclusive. Other attributes distinguishing the two genera, including the shape of the symphyseal region, are not preserved on the specimen. In the shape of the crowns and lack of occlusal striae, the fossil is unlike any species of either *Cyclodomorphus* or *Tiliqua* examined in this study, but it is too fragmentary to either allocate to a genus with certainty or to warrant description as a new taxon.

Family VARANIDAE Gray, 1827

?*Megalanina* sp.

Material examined

Five isolated dorsal vertebrae (WPC 115, 116, 2409, 2014, 3322), three isolated dorsal fragments (WPC 2040, 3555, 3556), four isolated caudal vertebrae (WPC, 1429, 1573, 2364, 2524).

Characters

The genus *Megalanina* is characterised in part by having massive thoracic and lumbar vertebrae with weakly developed zygosphenes (absent in typical *Varanus*) as well as small depressed neural canals. The adult teeth of *Megalanina* are large and slightly recurved distally. The anterior cutting edge is rounded and serrated distally. The posterior cutting edge is thin, blade-like and serrated along its entire length (Hecht 1975).

Description

The dorsal vertebrae are much more massive than those of any extant varanid but compare well in morphology with those from an extant varanid *Varanus varius* (AR 7641) as well as from large fossil varanids from the Bluff Downs Local Fauna (Appendix 2; Tables 1 and 2). The Chinchilla specimens are 62% larger than those measurements supplied for Australia's largest extant varanid, the perentie *Varanus giganteus* by Smith (1976) and 20% larger than those for the

large fossil varanid from Bluff Downs Local Fauna (Mackness & Hutchinson 2000).

Remarks

A single maxilla (QM F874) from the Chinchilla Sand was referred to *Varanus dirus* (Hecht 1975), a taxon originally described by De Vis (1889) on the basis of an isolated tooth from the Pleistocene Kings Creek locality. Hecht (1975) synonymised *V. dirus* with *Megalanina prisca*. Four isolated vertebrae (two caudals and two dorsals) have also been collected from the Chinchilla Sand and, although Hecht (1975) referred them to *Megalanina*, he also suggested that this material may represent a separate Pliocene species.

The assignment of the larger varanid vertebrae described in this paper to ?*Megalanina* is done purely on the basis of convention. Opinion is divided as to the current status of the genus, with Hecht (1975) and Molnar (1990) concluding it is valid but Estes (1983) and Lee (1996) suggesting that *Megalanina* should be synonymised with *Varanus*. A large collection of varanid fossils from Pliocene localities is presently under study by the authors.

Varanus sp.

Material examined

Two isolated dorsal vertebrae (WPC 118, 1430), one isolated caudal vertebra (WPC 3557).

Characters

These vertebrae are identified as varanid by their distinctive condyle-cotyle articulations. The dorsal vertebrae also show the characteristic constriction of the centra anterior to the condyle seen in *Varanus*.

Description

The vertebrae show characteristic varanid morphology with a range of centra lengths (Appendix 2; Table 3) that indicate a medium-sized goanna of the size of *Varanus gouldii*.

Remarks

Although Wilkinson (1995) suggests some characters for separating varanid species on the basis of vertebral morphology, many of these rely on the neural spine being present. This feature is missing on all three fossil vertebrae. Interspecific and/or intraspecific variation in varanid vertebrae have yet to be fully tested; therefore, characters

identified by Wilkinson (1995) must be used with caution.

DISCUSSION

The composition of the lizard fauna from the Chinchilla Sand Local Fauna, at least at family level (Appendix 2; Table 4), is similar to that of the Bluff Downs Local Fauna. This is the only other Australian Pliocene locality with a significant lizard record (Mackness & Hutchinson 2000). It differs from Bluff Downs in the generic representatives of each family, but the significance of this is unknown; it could merely be stochastic, reflecting the very small sample sizes at each locality. The palaeoenvironment was primarily fluvial for Chinchilla and lacustrine and fluvial for Bluff Downs.

The exact nature of the Chinchilla palaeoecology has yet to be determined. While there may have been a significant wetland component, as suggested by the presence of various aquatic taxa such as turtles (Gaffney 1981; Gaffney & Bartholomai 1979) and waterbirds (Olson 1975, 1977), there is also evidence that the environment was highly seasonal (Mackness et al 1999; Wroe & Mackness 2000). The presence of arboreal species such as *Koobor* (Archer 1977) and an unnamed phascolarctomorph (Mackness et al 1994) would be consistent with a complex and mature forest, but the composition of the mammalian fauna indicates a lack of undoubted

closed-forest species. Further, the predominance of grazing kangaroos and diprotodontids suggests that grasslands were also part of the environment.

The presence of an extinct reptile species at Chinchilla is noteworthy given the slow rate of faunal turnover in reptile populations (La Duke 1991). *Tiliqua wilkinsonorum* represents a distinctive but extinct species of lizard, a relatively uncommon observation for the Pliocene (Estes 1983). A conclusion that can be drawn from the presence of such 'fossil endemics' is that they signal ecological or geographical factors at Chinchilla during the Pliocene that are no longer present in recent environments.

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APPENDIX 1

Osteological material used for comparisons. Specimens are from the Herpetology Section of the South Australian Museum and the Western Australian Museum (WAM prefix).

Gekkonines

Christinus marmoratus (R35562; R39934), *Cosymbotus platyrus* (R36789), *Cyrtodactylus lousiadensis* (R14002), *Gehyra australis* (R34136), *G. dubia* (R42872), *G. sp.* (2n = 44) (R44595), *G. catenata* (R35561), *G. oceanica* (R08687), *G. purpurascens* (R36377), *G. robusta* (R34222), *Gekko gecko* (R35559), *G. japonicus* (R07435), *G. vittatus* (R55978) *Gonatodes humeralis* (R40088), *Gymnodactylus darwinii* (R40090), *Hemidactylus frenatus* (R35564), *Heteronotia binoei* (R09751 A, R33565, R39935), *Nactus cheverti* (R09740 B), *Paroedura picta* (R55105), *Phelsuma madagascariensis* (R40025), *Ptyodactylus hasselquisti* (R49804), *Tarentola annularis* (R40024), *Thecadactylus rapicauda* (R40099–100).

Diplodactylines

Bavayia ornata (R06752), *Crenadactylus ocellatus* (R03113 C), *Diplodactylus byrnei* (R13514), *D. conspicillatus* (R19967), *D. damaeus* (R20017, R24553) *D. 'granariensis'* (SA populations) (R02010, R26494, R29135), *D. immaculatus* (R42676), *D. pulcher* (R26383), *D. steindachneri* (R05153, R52746), *D. stenodactylus* (R07592, R21240, R26777), *D. tessellatus* (R03876, R40938), *D. vittatus* (R35568), *Hoplodactylus pacificus* (R11025), *Nephurus asper* (R35567), *N. laevis* (R00309 A, R27044–45), *N. milii* (R55422, R57083), *N. stellatus* (R32297), *Oedura lesueurii* (R33597), *O. marmorata* (R42893), *O. monilis* (R35563), *O. tryoni* (R33583), *Phyllurus platurus* (R35054), *Rhynchoedura ornata* (R35827), *Saltuarius swaini* (R29205), *Strophurus ciliaris* (R10697, R35566), *S. intermedius* (R14325 C).

A range of pygopod skulls was also examined (see Hutchinson 1997 for listing).

Egernia group skinks

Corucia zebrata (R35765), *Cyclodomorphus maximus* (WAM R77193, WAM R77637), *C. michaeli* (R35682), *C. gerrardii* (R35761, R47699), *C. melanops elongatus* (R03231, R03856 G, R35681), *C. venustus* (R38021), *Egernia coventryi* (R35686, R47693–94), *E. cunninghami* (R35680, R35763), *E. depressa* (R03433 H), *E. formosa* (WAM R65803), *E. hosmeri* (R22510), *E. inornata* (R07234, R07238, R07245 A, R35687), *E. kingii* (WAM R36376, WAM R89269–70), *E. luctuosa* (WAM R36019), *E. major* (R27043, R35762), *E. multiscutata* (R08469, R25245), *E. napoleonis* (R35692, R51076, WAM R45350), *E. pilbarensis* (WAM R78945), *E. pulchra* (R40026, WAM R71884), *E. richardi* (R10841), *E. saxatilis intermedia* (R43961), *E. stokesii* (R02560, R41913), *E. striata* (R07179, R07198), *E. striolata* (R02909 B, R16593, R26891, R38019), *E. whitii* (R02726, R35690, R27042, R35689, R45316, R34886, R35688, R35691), *Tiliqua adelaidensis* (R40738, R40745, R43412), *T. gigas* (R11419), *T. multifasciata* (R27041, R35757), *T. nigrolutea* (R02725, R27048, R27050, R47698), *T. occipitalis* (R02724, R25369, R27047, R35758), *T. rugosa* (R02563[2], R02564, R27026, R27028, R02801, R25615, R27027, R27029, R27584, R31855, R35760), *T. scincoides* (R02561, R27036–40, R35759, R38020, R43962, R27094).

APPENDIX 2

TABLE 1. Measurements (mm) of ?*Megalania* dorsal vertebrae from Bluff Downs and Chinchilla Local Faunas compared with *Varanus giganteus*. Measurements as defined in Methods. Range (mean \pm standard deviation). Data for *V. giganteus* taken from Smith (1976), for Bluff Downs from Mackness & Hutchinson (2000).

Specimen	No	Pr-Po	BW/Pr-Po	CW/Pr-Po	Pr-Pr/Pr-Po
<i>V. giganteus</i>	20	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)
Bluff Downs	7	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)
Chinchilla	4	24.5–27.1 (25.7 \pm 0.14)	0.54–0.64 (0.58 \pm .005)	0.55–0.63 (0.59 \pm .006)	0.88–1.01(0.92 \pm .007)

TABLE 2. Measurements (mm) of individual ?*Megalania* vertebrae. Measurements as defined in Methods.

Specimen	Pr-Po	Pr-Pr	Po-Po	BW	CW	COW	CEL
WPC116	39.4	33.2	39.3	20.5	26.1	27.6	25.0
WPC2014	38.9	46.4	41.4	—	—	30.4	—
WPC2409	48.3	57.3	49.5	26.4	29.4	31.6	28.2
WPC3322	37.2	43.5	40.4	17.6	23.2	25.2	26.4
WPC3555	56.8	—	—	—	—	—	—
WPC3556	44.3	—	—	—	—	—	—
(Mean/SD)	(41.6 \pm 6.6)	(47.6 \pm 6.6)	(42.6 \pm 4.6)	(21.5 \pm 4.5)	(26.2 \pm 3.1)	(28.7 \pm 2.9)	(26.5 \pm 1.6)

TABLE 3. Measurements (mm) of centra of dorsal vertebra of fossil *Varanus* sp. from Chinchilla Local Fauna (WPC), Bluff Downs Local Fauna (QMF) and extant *Varanus varius* (AR7641).

Specimen	Measurement	Specimen	Measurement
WPC118	12.2	AR7641 (a)	15.3
WPC1430	16.5	AR7641 (b)	15.3
QM F7774	14.2	AR7641 (c)	15.4
QM F23238	10.5	AR7641 (d)	15.4
QM F23659	10.8	AR7641 (e)	15.6
QM F23683	13.8	AR7641 (f)	15.7

TABLE 4. Comparison of lizard taxa recovered from the Queensland Pliocene (Chinchilla and Bluff Downs Local Faunas. Source: Mackness & Hutchinson 2000). Code: present •, absent x, endemic form ^(e).

Taxa	Chinchilla	Bluff Downs
Gekkonidae		
<i>cf Heteronotia</i>	x	•
<i>Diplodactylus</i>	• ^(e)	x
Agamidae		
unidentified material	•	•
Varanidae		
? <i>Megalania</i>	•	•
<i>Varanus</i>	•	•
Scincidae		
<i>Tiliqua</i>	• ^(e)	•
<i>Cyclodomorphus</i>	•	x
<i>Egernia</i>	x	•
<i>Eulamprus</i>	x	•

FIRST REPORT OF THE CUPRESSACEAN CONES IN THE EOCENE EYRE FORMATION OF SOUTH AUSTRALIA

N. S. PLEDGE

Summary

Conifer impressions are a very minor component in the various 'silcrete flora' assemblages found in the interior of South Australia. Previously, no fruiting bodies had been found, although numerous foliage species have been recognised. This note describes impressions of the first woody ovulate cones found, discovered in a small block of silicified sandstone near Lake Hart, west of Woomera. They are distinctive and do not appear to bear close affinity to any modern Australian species, but resemble cones of the African *Widdringtonia*.

FIRST REPORT OF CUPRESSACEAN CONES IN THE EOCENE EYRE FORMATION OF SOUTH AUSTRALIA

NS PLEDGE

PLEDGE, NS. 2002. First report of cupressacean cones in the Eocene Eyre Formation of South Australia. *Records of the South Australian Museum* 35(2): 185–191.

Conifer impressions are a very minor component in the various 'silcrete flora' assemblages found in the interior of South Australia. Previously, no fruiting bodies had been found, although numerous foliage species had been recognised. This note describes impressions of the first woody ovulate cones found, discovered in a small block of silicified sandstone near Lake Hart, west of Woomera. They are distinctive and do not appear to bear close affinity to any modern Australian species, but resemble cones of the African *Widdringtonia*.

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Besides *Athrotaxis*, the modern Australian flora contains three genera of cupressacean conifers: *Callitris*, *Actinostrobus* and *Diselma*. Recent morphological and molecular work by Gadek et al (2000) shows that the latter are closely related to an African genus *Widdringtonia*, within a monophyletic group, the subfamily Callitroideae, comprising all Southern Hemisphere cupressaceans except *Athrotaxis*.

Fossil conifers, including members of the Cupressaceae, are sparse in the Australian fossil record (Hill & Carpenter 1989). Many reported specimens have occurred as impressions in fine-grained sediments, with consequent difficulty in interpreting fine structure, but organic remains also occur, eg in Tasmania, and have yielded valuable material (ibid). This has more than doubled the number of genera in the Australasian region, with taxa that occur today in New Guinea, New Zealand and elsewhere, as well as several extinct genera (Hill & Brodribb 1999).

Plant impressions in silicified sandstone have been known from the Woomera area / Arcoona Plateau for many years (Chapman 1937), and as far as Stuart Creek to the north and Clayton Station on the Birdsville Track to the northeast. Most of the moulds are of angiosperm leaves (Rowett 1997), a few of which have been described (Chapman 1937; Greenwood et al 2001). Conifer vegetative shoots are a minor unobtrusive component, studied by Nunn (1964) and Offler (1969, 1984). In the 1970s localities were found yielding natural moulds of fruiting bodies, mostly of myrtaceous origin (Ambrose et

al 1979; Lange 1978). A few specimens referable to fruit of Proteaceae (*Banksia* sp.) and Casuarinaceae have been noted (Greenwood et al 2001; this writer, unpubl.) but, until now, no coniferous cones have been recognised, despite the widespread occurrence of vegetative shoots. Nunn (1964) recognised 21 different conifer morphotypes, some of which could be related to modern species from the Australasian region. She stressed the problems and uncertainties of identifying the species.

These plant fossil impressions occur in a number of isolated, discrete localities over an area of thousands of square kilometres, often in apparent channel deposits, eg at Nurrungar, Island Lagoon, near Woomera (pers. obs. 1969), in what has been regarded as Eyre Formation s.l. Their age has long been in dispute (Ambrose et al 1979; Callen & Lange 1986; Chapman 1937; Greenwood et al 1990; Wopfner et al 1974) but recent discoveries at Nelly Creek, Lake Eyre South, have at last related them to deposits datable by palynological studies to the middle Eocene (Alley et al 1996; Callen & Cowley 1995; Christophel et al 1992) within the Eyre Formation. Variations in the contained fossil floral assemblages suggest that the different localities probably have slightly different ages.

MATERIAL AND METHODS

In 1979 members of the Woomera Natural History Society discovered plant impressions near



FIGURE 1. Locality map, Lake Hart and other 'silcrete flora' localities in South Australia.

Lake Hart in the Woomera Prohibited Area (Fig. 1). Subsequently, L. Marsh and T. Nurenberg presented a slab of quartzite to the South Australian Museum (SAM P22732; Fig. 2) bearing the impressions of a few leaves and seven fruit-like bodies. Silicone rubber casts (Fig. 3) taken from these moulds disclosed fruits strongly reminiscent of *Callitris* ovulate cones. Closer examination, however, showed that, instead of the six subequal valve scales (2 triplets) seen in *Callitris*, these fruit had two unequal pairs of valves (Fig. 4). Re-examination of the collection of silcrete flora material in the Museum failed to uncover any further specimens; SAM P22732 is therefore unique.

Comparison was made with dried specimens in the South Australian State Herbarium and with trees growing at the Mount Lofty Botanic Gardens.

DESCRIPTION

Order CONIFERALES

Family CUPRESSACEAE Neger

Genus *Incertae sedis*

The cones are globose to ellipsoidal in shape, with a slightly conical distal apex. The ellipsoidal shape may be due to slight compression during burial, but the flattening is always the same relative to the smaller valve scales and symmetry of the cone, and compression is therefore an unlikely cause. Dimensions vary from about 17 mm diameter and a length of up to 22 mm for the globose forms, to 15–22 mm diameter x 20 mm in length for the ellipsoidal specimens. In apical view the pair of larger valves are at the ends of the apparent ellipse. The smaller, narrower, valves meet apically along a contact line of about 5 mm, thus separating the pair of larger valves (Fig. 4). Although apparently mature, the cones have a relatively smooth surface, with none of the roughness that characterises the opened cones of many *Callitris* species. However, one cone, at least, shows slight apically convergent ribs on the valves. This is reflected in an impression of what appears to be a decorticated cone (Fig. 3), having exposed ribs that have the same symmetry and relationships as the valves. None of the fruits has split to release its seeds, so the extent of the sutures separating the valves may not be fully expressed. Nevertheless, the sutures extend slightly more than halfway towards the base. The valves each have a near-apical, small (roughly 1 mm), circular to elliptical scar, arranged symmetrically on the fruit (Fig. 4). The origin or purpose of these scars is unclear, although they are in the same position as the 'spurs' on the valves of some species of *Callitris* (Baker & Smith 1910: 47) and species of *Papuacedrus*, *Widdringtonia* and *Tetraclinis* (pers. obs.; Hill & Carpenter 1989; McIver 2001). The base and attachment are seen in one specimen, showing a petiole expanding gradually to about 5 mm diameter at its junction with the fruit, where there is an expanded leaf scale below the smaller valve (Fig. 4). Another specimen seems to show a 7–8 mm diameter subcircular scar on the base, where the stem attached.

Comparisons

Initial comparisons were with species of *Callitris*. The obvious difference is in the number

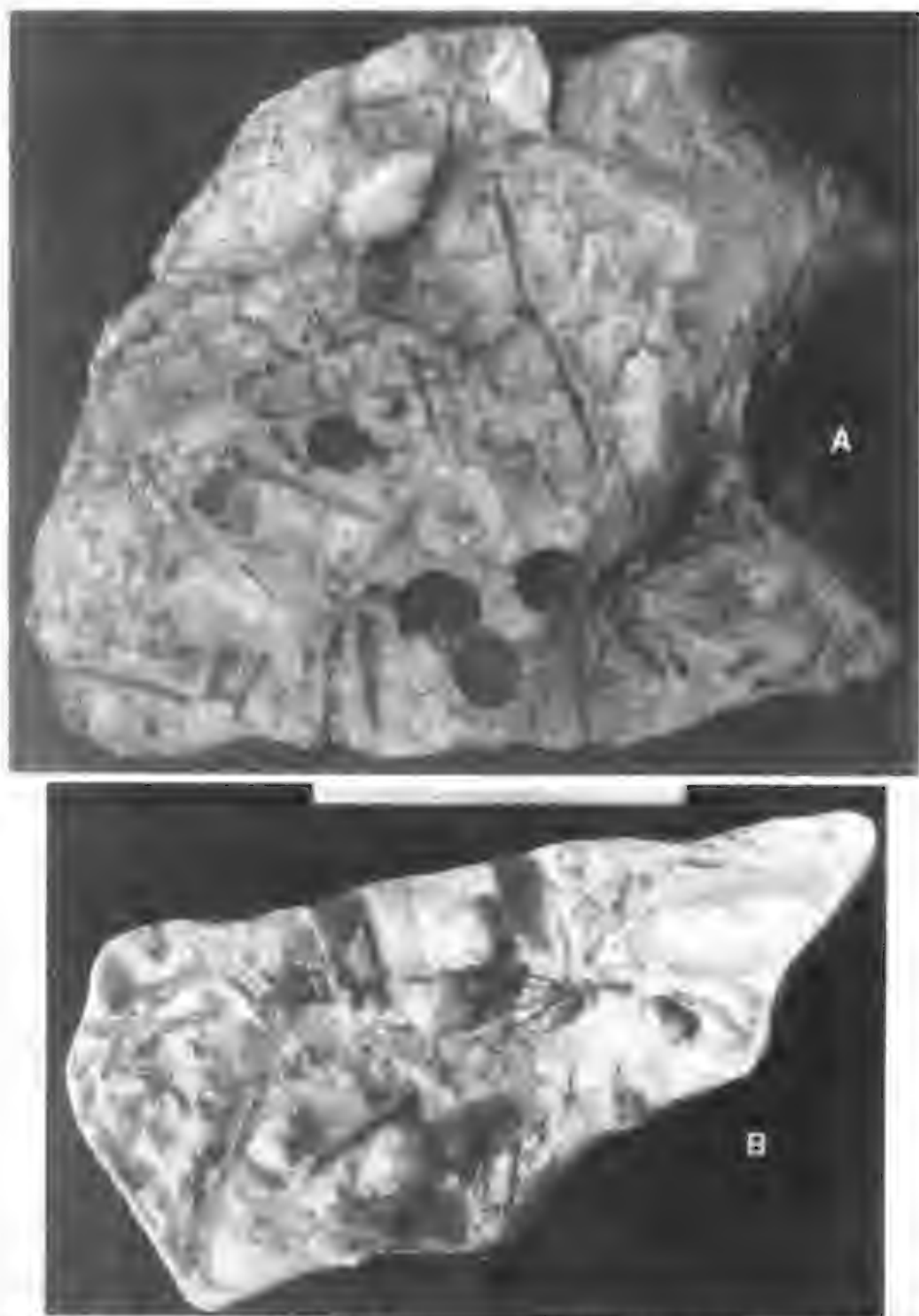


FIGURE 2. A, the fossil slab, SAM P 22732. B, positive cast of part of the slab, replicating the original appearance of the leaf litter at the time of burial. Scale in mm.

of valves in the cones, *Callitris* having three large valves alternating with three smaller ones, all ending acutely. Amongst living Australian conifers, there is only one species having two pairs of valves in the same decussate geometry as the fossils: *Diselma archeri* from Tasmania. However, its ovulate cones are tiny, barely larger in diameter than the shoots they terminate (pers. obs.). The living *Papuacedrus* from the island of

New Guinea also has two pairs of valves, but its cones too are small and conical (Hill & Carpenter 1989).

A passing note in Baker and Smith (1910) directed attention to several non-Australian genera. *Diselma* had once been synonymised with *Fitzroya* from Chile and Patagonia, just as *Callitris* had been joined with *Tetraclinis* from Mediterranean North Africa and *Widdringtonia*



FIGURE 3. Positive silicone rubber cast of the better fossil cones, showing 1, cone with apical view of sutures and valves with terminal scars; 2, cone with attached stem and basal leaf-scale; 3, cone with basal attachment scar; 4, a decorticated cone; 5, foliage fragment. Scale in mm.

spp. from southern Africa. I was not able to see fruits of *Fitzroya*, but am informed that they are nothing like the fossils (R. Hill, pers. comm., July 2002). Through the help of Ms H. Vonow at the South Australian Herbarium, I examined dry specimens of *Diselma archeri*, *Tetraclinis articulata*, *Widdringtonia cupressoides*, *W. whytei* and others and *Papuacedrus papuana*, and living *Widdringtonia* spp. in the Mount Lofty Botanic Gardens. There is an obvious similarity between

these species and the fossil cones in the number and symmetry of the valves. However, *Tetraclinis* can be removed from consideration on the basis of two characters; the spurs near the tips of its valves are quite enlarged, particularly on immature cones (there is obviously some allometric growth involved here), and the foliage structure is quite different from the fossil shoot associated with the cones. Offler (1969) indicates that *Papuacedrus* foliage is widely represented in her material, and



FIGURE 4. Detail of cones: silicone rubber cast, showing 1, cone with apical view of sutures and valves with terminal scars, 2, cone with attached stem and basal leaf-scale, 3, cone with basal attachment scar, 4, foliage fragment.

it has been recognised in the Eyre Formation of the Poole Creek Palaeochannel near Lake Eyre South (Alley & Pledge 2000: 69). Fossil foliage has also been recorded from various Oligocene and Miocene sites in Tasmania (Hill & Brodribb 1999; Hill & Carpenter 1989). However, *Papuacedrus* differs considerably from the fossils in the tear-drop shape and small size of the cones, and in the presence of bract-like appendages halfway up each cone scale (Hill & Carpenter 1989).

There are two genera considered closely related to *Papuacedrus*, namely *Libocedrus* from New Zealand and New Caledonia, and fossil in Tasmania, and *Austrocedrus* from South America and also fossil in Tasmania (Hill & Carpenter 1989). They have ovulate cones of the same order of size as *Papuacedrus* (and therefore are much smaller than the Lake Hart fossils) but are similar in having a structure subapically on the abaxial surface of each cone scale: a spine in the case of *Libocedrus* and a minute tubercle in *Austrocedrus* (ibid). However, the cone scales of *Austrocedrus* are all apically acute with none truncated; therefore, that genus can probably be ruled out of contention.

The woody ovulate cones of the *Widdringtonia* spp. vary between species in both size and morphology. Like the fossils, they have two unequal pairs of valve scales, the upper pair having truncated apices that therefore meet along a contact of several millimetres. Of those examined, cones of *W. cupressoides* (Fig. 5) resemble the fossils most closely, although they tend to be smaller and have more prominent spurs on the valves, and the overall shape is more tulip-like, with a depressed base. Other species show a rougher, more rugose and warty or tuberculose surface on the valves than do the fossils, but this may be a reflection of the maturity of the fruit. The Lake Hart fossils differ markedly from the North American Cretaceous species *Widdringtonia americana* (McIver 2001), primarily in the development of a prominent umbo or boss on each valve scale in the latter species.

The vegetative shoot (Figs 3, 4) associated with the fossil cones is poorly preserved (the grain-size of the sediment approaching that of the smaller features), and cannot be guaranteed to relate to the cones. It seems to have the same square cross-section and short decussate, scale-like leaves as *Diselma archeri* (Clifford & Constantine 1980). This is unlike *Widdringtonia cupressoides*, which has shoots of rounder cross-section and longer decussate leaves. The leaves are apparently arranged in opposite pairs, as in *Libocedrus* and

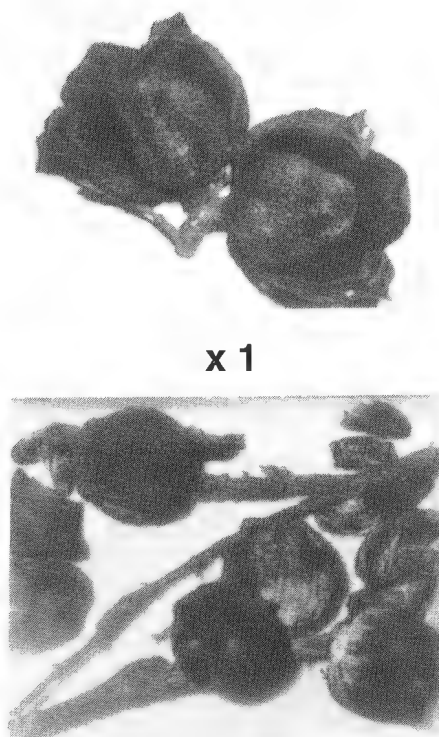


FIGURE 5. Female cones of *Widdringtonia cupressoides* (L.) Endlicher, specimens from the South Australian Herbarium collections.

Papuacedrus (Hill & Carpenter 1989). Unfortunately, no other specimens from this site are available to support or deny this association, and the locality has reportedly been stripped by commercial interests for decorative stone.

CONCLUSIONS

It is apparent that these impressions represent the fruiting bodies of a previously unknown Australian species of conifer, and it is suggested that this shows closest affinities with species of *Widdringtonia*, *Diselma* and *Papuacedrus*. Without corroborative evidence in the form of organically associated foliage and pollen, it is not possible to specify which taxon the cones represent; no identification is proposed, but it could be a new extinct genus. *Widdringtonia* today inhabits seasonally dry to semi-arid regions of southern Africa (Hill & Brodribb 1999), as do *Callitris* spp. Such an environment is implied (Alley et al 1996) for part of the Eyre Formation. In view of the fact that Offler (1969) found no

trace of either *Callitris* or *Actinostrobus* foliage in the 'silcrete flora' of the Woomera area, that no cones of *Callitris* have subsequently been found in the large collections made since her study, and that there have been only a few finds of fossil *Callitris* foliage in southeastern Australia (Hill & Brodribb 1999), it is suggested that these typical Australian genera evolved subsequently, possibly from a form like the fossil taxon described here.

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**DESCRIPTIONS OF A NEW GENUS AND TWO NEW SPECIES OF
VIVIPARID SNAILS (MOLLUSCA: GASTROPODA: VIVIPARIDAE) FROM
THE EARLY CRETACEOUS (MIDDLE-LATE ALBIAN) GRIMAN CREEK
FORMATION OF LIGHTNING RIDGE, NORTHERN NEW SOUTH WALES**

ROBERT J. HAMILTON-BRUCE, BRIAN J. SMITH & KAREN L. GOWLETT-HOLMES

Summary

Fossil gastropods belonging to the family Viviparidae (Caenogastropoda (Prosobranchia)) are described from the Early Cretaceous (middle-late Albian) Griman Creek Formation of Lightning Ridge, northern New South Wales. From our research, this is the earliest definitive record of non-marine gastropods from Australia and among the oldest viviparid material in the world recorded to date. A new genus and two new species are described, and other material attributable to the extant genus *Notopal* is recorded. Implications for the current distribution of the Viviparidae are addressed.

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HAMILTON-BRUCE, RJ, SMITH, BJ & GOWLETT-HOLMES, KL. 2002. Descriptions of a new genus and two new species of viviparid snails (Mollusca: Gastropoda: Viviparidae) from the Early Cretaceous (middle-late Albian) Griman Creek Formation of Lightning Ridge, northern New South Wales. *Records of the South Australian Museum* 35(2): 193–203.

Fossil gastropods belonging to the family Viviparidae (Caenogastropoda (Prosobranchia)) are described from the Early Cretaceous (middle-late Albian) Griman Creek Formation of Lightning Ridge, northern New South Wales. From our research, this is the earliest definitive record of non-marine gastropods from Australia and amongst the oldest viviparid material in the world recorded to date. A new genus and two new species are described, and other material attributable to the extant genus *Notopala* is recorded. Implications for the current distribution of the Viviparidae are addressed.

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Opalised fossils have long been known from the Lower Cretaceous (middle-late Albian) freshwater deposits of the Griman Creek Formation, Lightning Ridge, New South Wales (Smith 1999). To date, much of the published work has focused on fish (Kemp 1991; Kemp & Molnar 1981) and terrestrial tetrapod remains (Archer et al 1985; Flannery et al 1995; Molnar 1980a, 1980b, 1991; Molnar & Galton 1986; Rich et al 1989) with relatively few reports (Dettman et al 1992; McMichael 1957; Smith 1999) summarising the vast quantities of invertebrate material recovered from the area. The recent opportunity to examine Lightning Ridge gastropod specimens (brought to our attention by Ben Kear, South Australian Museum, as part of an ongoing assessment of vertebrate and invertebrate fossil material from the locality) from the collections of the Australian Museum, Sydney, and several private individuals has prompted a systematic appraisal of the gastropods within the material recovered. This study describes specimens attributable to the family Viviparidae (Caenogastropoda (= Prosobranchia)), including a new genus and two new species. Indeterminate material belonging to the extant genus *Notopala* is also recorded, and the implications for

distribution of extant viviparid taxa are discussed.

The Viviparidae is a cosmopolitan group of freshwater caenogastropods, characterised by medium- to large-sized turbiniform shells which possess a rounded body whorl; moderately high, pointed spire; wide, round aperture; and sub-spiral, horny operculum (Smith 1992). The current Australian distribution of the group is limited to a few species occurring in the large drainage basins that span much of the arid centre and northern tropical regions of the continent.

The fossil record for Viviparidae is known from the Jurassic to Recent (*Viviparus* Montfort, 1810), with a tentative report based on an internal shell (?*Bernicia* Cox, 1927) mould (possibly of marine origin) from the Lower Carboniferous of England (Brookes-Knight et al 1960). Within Australia there are few records of fossil viviparids. Etheridge (1902) described the earliest potential Australian taxon, *Viviparus* (?) *alba-scopularis* Etheridge (also noted by Newton (1915)) from the Aptian marine deposits of the Doncaster Member (Wallumbilla Formation *sensu* Burton & Mason 1998), White Cliffs, New South Wales. This specimen is currently under examination by the authors and at present is regarded as being of unclear viviparid affinity. Cotton (1935a) erected

a species of *Notopala* (*N. wanjacalda*) from late Pleistocene sediments along the Murray River near Sunnyside, South Australia, and also noted a second taxon (*Notopala* sp.) from the same deposits, which showed strong similarity to the extant *N. hanleyi* (Frauenfeld, 1862). Viviparid snail shells from Early Cretaceous deposits in the Lightning Ridge area were recorded but not described by Dettman et al (1992) and Smith (1999); the latter also recorded possible representatives of the Naticidae, Thiaridae and Ellobiidae. Few other Australian non-marine gastropod fossils (all of Tertiary age) have been recorded (Archer et al 1994; Arena, 1997; Chapman 1937; McMichael 1968).

MATERIALS AND METHODS

All specimens described herein are derived from the Lightning Ridge opal fields (exact mine localities from which these specimens originated are unknown), Surat Basin, northwestern New South Wales. The opal-bearing sediments in this area form part of the Griman Creek Formation, a unit dated as middle-late Albian in age (Dettman et al 1992). The deposit predominantly reflects a coastal plain facies (Burger 1988; Dettman et al 1992) situated in an Early Cretaceous high latitude zone (~70° S, Embleton 1984). Invertebrate fossils, plant root impressions and vertebrate taphonomy suggest a freshwater estuarine to lacustrine setting (Dettman et al 1992; Molnar 1980a). Palaeoclimatic indicators imply strongly seasonal conditions with sea-level isotopic palaeotemperatures in the Eromanga Basin / Surat Basin regions ranging from 11.9°C (northeast) to 16.3°C (southwest) (Dettman et al 1992; Stevens & Clayton 1971).

Designation of parietal fold position on the specimens was achieved by positioning the fold within the aperture on a 360° compass setting when a vertical line through the axis, juxtaposed to the column, is intersected by a horizontal line corresponding to the midpoint of the aperture. The adapical axis above the point of intersection is taken as zero degrees. The diameters of all shells were measured following the method of Boycott (1928) and are defined as 'the greatest dimension that can be found starting with the edge of the lip to a point on the opposite side of the shell on the last whorl'. To enable extrapolation of the numbers of missing whorls, the incremental angle of the shells was judged by drawing a line so as to touch each of the

present whorls across each side of the shell; the point at which they met was assessed as being approximately the original apex of the shell (Cox 1960). All specimens are deposited in the Australian Museum (AM), Sydney. All specimens were prepared using a diamond drill-bit attached via a flexible lead to a high-speed rotary motor. Shell measurements were made to the nearest 0.05 mm using dial calipers.

SYSTEMATICS

Class GASTROPODA

Subclass ORTHOGASTROPODA

Superorder CAENOGASTROPODA

Order ARCHITAENIOGLOSSA

Superfamily AMPULLARIOIDEA

Family VIVIPARIDAE Gray, 1847

Diagnosis

Medium to large dextral, turbiniform shells, body whorl rounded, spire moderately high, pointed; aperture wide, round, parietal fold present or absent; operculum horny, subspiral (modified after Smith 1992).

Remarks

The above diagnosis follows Smith (1992), modified to accommodate the presence of a parietal fold in the new genus described below. Viviparid snails are, as their name suggests, viviparous (live bearing) and are found in both lotic and lentic systems throughout the world (Browne 1978). Within Australia the family is currently represented by the extant native genera *Notopala*, *Larina* and *Centropala* (Smith 1992). A species accidentally introduced from Asia, *Bellamya heudei guangdongensis* (Kobelt, 1906), recorded by Shea (1994) as established in New South Wales, is not considered part of the Australian fauna in this study. The Australian members of the family have undergone substantial revision over many years (Cotton 1935a, 1935b; Sheldon & Walker 1993; Stoddart 1982); the use of intraspecific shell variation and morphometric data by recent authors has resulted in a substantial reduction in the numbers of accepted species. Shell colouring and pattern and the form of the operculum, which are important characters in

determining generic placement in this family, are characters lost in most fossils.

The present specimens from Lightning Ridge are over 100 million years old (Albian [108–97.5 Ma]) and totally opalised. While sculpturing on some specimens has been preserved, colour bands and opercula have not; therefore, only structural shell characters could be used to assign them to taxa. Two major factors have been taken into account before deciding to place them in Viviparidae — the shell morphology, which fits within the currently accepted diagnosis of the family with only slight modification (the presence of the parietal fold in the two new species); and the freshwater depositional environment from which they originated. Whilst all the specimens can be accommodated within the family Viviparidae, those possessing a parietal fold cannot be assigned to any currently recognised genus and are considered to belong to a new genus which is described below. Direct comparisons between species, living or fossil, are few (Brown 1980); however, due to the lack of colour patterns and opercula as well as soft parts in these fossils, the only remaining methods are based on morphology. Therefore, we have applied parts of the morphometric data gathered by Sheldon and Walker (1993) to justify the placement of these specimens within Viviparidae, and in one case in the extant genus *Notopala*, and to offer a method of comparison between extant and extinct species. None of the data comparisons

are in any way intended to suggest relationships between members of either the *Notopala* sp. presented here or the new genus and any extant species.

Genus *Albianopalin* gen. nov.

Diagnosis

Shell dextral, thick, solid, globose to subglobose, ventricose, three–five whorls, subumbilicate; aperture subovate, large, approximately equal to height of spire; parietal fold present, simple. Operculum unknown.

Type species

Albianopalin benkeari sp. nov.

Etymology

From the combination of *Albian*, n. referring to age of the Lower Cretaceous opal-bearing deposits of the Griman Creek Formation, and *opalin*, Middle English, from *opalus*, Latin, alteration of Greek *opallios*, for 'opal'.

Remarks

While this new genus has similarities to *Notopala* (Cotton, 1935b), *Albianopalin* gen. nov. is easily separated from *Notopala* and all other genera within the family by the presence of a parietal fold in the basal lip, currently a feature unique to this genus within the family.



FIGURE 1. AMF122185 *Albianopalin benkeari* sp. nov. in A, apertural and B, dorsal views.

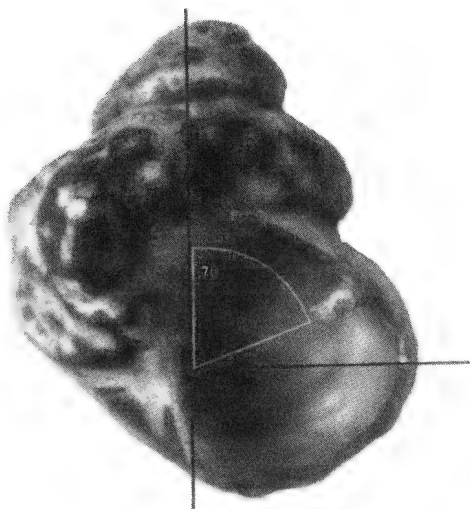


FIGURE 2. AMF122185 *Albanopalina benkeari* sp. nov. in apertural view showing angle of parietal fold.

Albanopalina benkeari sp. nov. (Figs 1, 2, Appendix)

Diagnosis

With the features of the genus; parietal fold simple, 70° from vertical axis.

Type specimen

Holotype: AMF122185 (Figs 1, 2, Appendix)

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle–late Albanian.

Description

Shell 17.7 mm high, 16.4 mm maximum diameter, dextral, turbiniform, subglobose. Teleconch with three complete whorls and broken parts, pointing to the possible presence of further whorls. Whorls impressed. Relatively evenly spaced spiral prosocyrta ornamentation present on many areas of teleconch. Aperture large (10.85 mm high), round; basal outer lip varicose with no evidence of eversion. A single, triangulated parietal fold (3.0 mm long, 1.0 mm wide, 2.0 mm deep) present on upper surface of basal lip, deepest side facing adaperturally (Fig. 2).

Etymology

Named for Ben Kear, for his assistance in this study.

Remarks

Holotype unique. The position of the parietal fold separates *A. benkeari* sp. nov. from the other new species described below. The holotype specimen is undistorted, but the spire is incomplete. Extrapolation from the spire angle indicates that there may have been at least four and as many as five complete whorls originally. Being opalised, the state of preservation of the holotype is very good, with much of its detailed surface ornamentation preserved.

Albianopalina lizsmithae sp. nov. (Figs 3, 4, Appendix)

Diagnosis

With the features of the genus; parietal fold simple, 112° from the vertical.

Type specimen

Holotype: AMF122186 (Figs 3, 4, Appendix)

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle–late Albanian.

Description

Shell, 15.1 mm high, 12.9 mm maximum diameter, dextral, turbiniform, subglobose. Teleconch with two complete whorls and broken parts, pointing to the possible presence of further whorls. Whorls impressed. This particular specimen has undergone some dorsoventral compression which has resulted in distortion, especially at base of final whorl. Aperture large (9.95 mm high), round; basal outer lip varicose with no evidence of eversion. A single, basal parietal fold (3.75 mm long, 2.3 mm wide, 2.2 mm deep) is present on surface of basal lip, deepest side facing adaperturally (Fig. 4). Spiral prosocyrta ornamentation present on parts of teleconch, especially proximal to aperture.

Etymology

We name this species for our colleague Elizabeth (Liz) Smith of the Australian Museum (AM), for her assistance in this study.

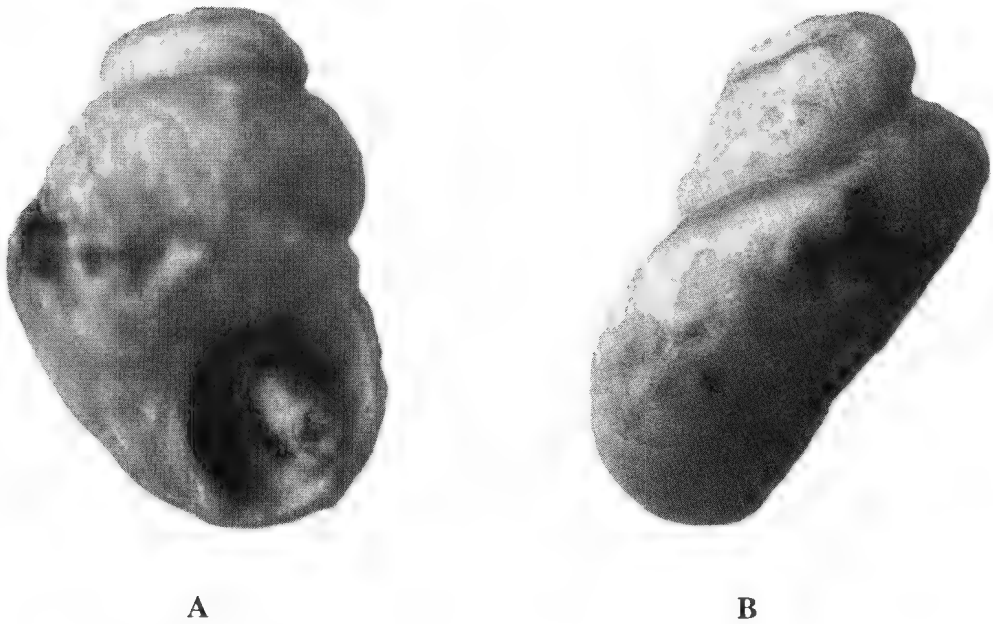


FIGURE 3. AMF122186 *Albanopalin lizsmithae* sp. nov. in **A**, apertural and **B**, dorsal views.

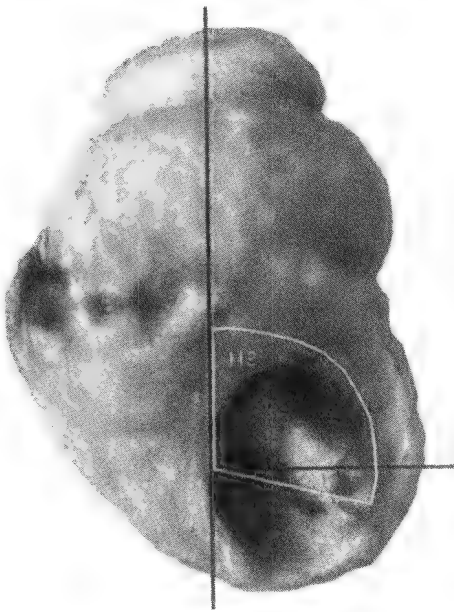


FIGURE 4. AMF122186 *Albanopalin lizsmithae* sp. nov. in apertural view showing angle of parietal fold.

Remarks

Holotype unique. The position of the parietal fold separates *A. lizsmithae* sp. nov. from *A. benkeari* sp. nov. as described above. The holotype has undergone moderate dorsoventral compression, resulting in the specimen appearing stretched. Like *A. benkeari* sp. nov., the spire is incomplete, and extrapolation from the spire angle indicates that there originally may have been at least four and as many as five complete whorls. Being opalised and having damage to parts of the surface of the teleconch, the state of preservation is good enough to preserve some of its detailed surface ornamentation.

Genus *Notopala* (Cotton, 1935b)

Type specimen

Type species: *Paludina hanleyi* (Frauenfeld, 1864) by original designation.

Diagnosis

Shell dextral, globose-conic, subumbilicate, five whorls, ventricose to angulate below the periphery; aperture subovate, large, about equal to height of spire; parietal fold absent; operculum corneous.

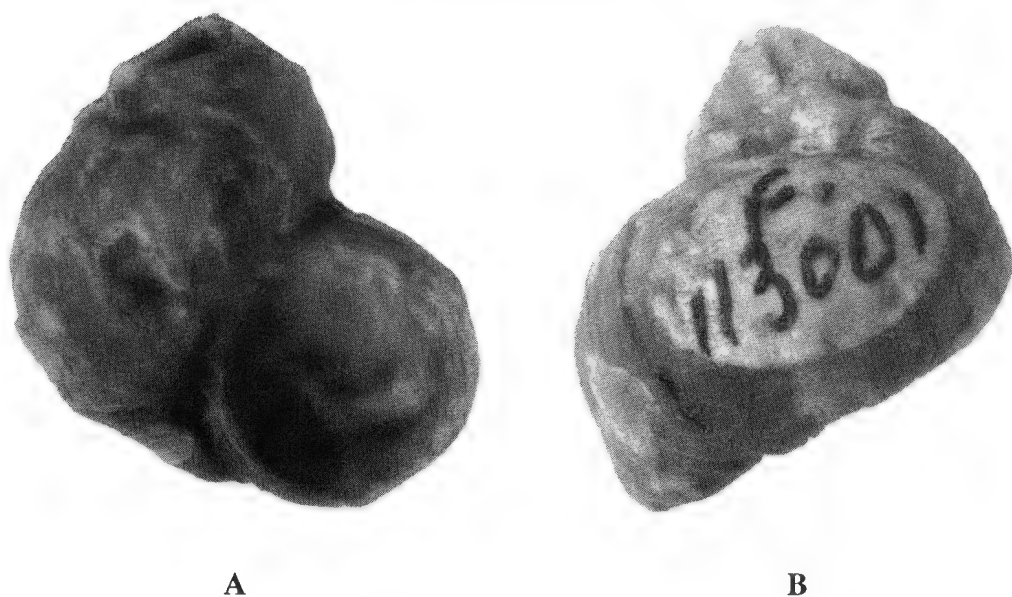


FIGURE 5. AMF13001 *Notopala* sp. in A, apertural and B, dorsal views.

Remarks

These specimens are extremely significant. Until their discovery, none of the currently living native Australian viviparid genera were known from deposits older than Plio-Pleistocene. This temporal range is now extended back to the Lower Cretaceous (middle-late Albian). It is also interesting to note that another living species, the lungfish *Neoceratodus forsteri*, has been recorded from the Griman Creek Formation of Lightning Ridge (Kemp & Molnar 1981).

Notopala sp. (Fig. 5, Appendix)

Referred material

AMF13001 (Fig. 5), AMF122166–AMF122184 (not figured herein).

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle-late Albian.

Description

Shell dextral, turbiniform, subglobose. Teleconch with two to three complete impressed whorls; the incremental angle of the shell indicates that there were originally four or five whorls. Aperture large, round; basal outer

lip varicose with no evidence of eversion.

Remarks

There is considerable variation in size, state of preservation, degree of corrosion and/or damage to the shells, opalisation, amount of matrix deposition on the shells, completeness of the aperture and presence/absence of ornamentation. We have not described these specimens as a new species at this stage. We feel that the exact taxonomic position of this material compared with other species in the genus requires further study. The preceding table (Table 1), diagram (Fig. 6, modified from Sheldon & Walker 1993) and graph (Fig. 7) show measurements of shell characters for each of the living Australian species of *Notopala*, and illustrate morphometric similarity of the specimens of *Albianopalin* nov. sp. as well as *Notopala* sp. described here to existing members of the genus. However, the specimens of *Notopala* sp. vary greatly in their physical condition, and it has not been possible to take the full range of measurements from each of the 20 specimens being studied. The reason for the inclusion of this data is not to demonstrate any relationship between extant species and the specimens from Lightning Ridge, but to show that the physical characteristics of the new material (*Albianopalin* sp. nov. and *Notopala* sp.) fit within the parameters for inclusion in the family Viviparidae.

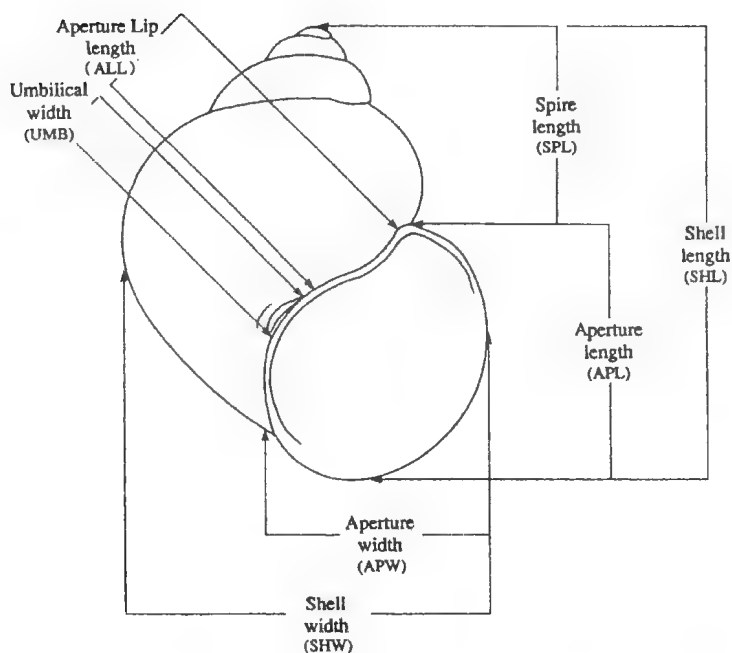


FIGURE 6. Diagram illustrating measurement parameters used in the morphometric analysis (modified from Sheldon & Walker 1993).

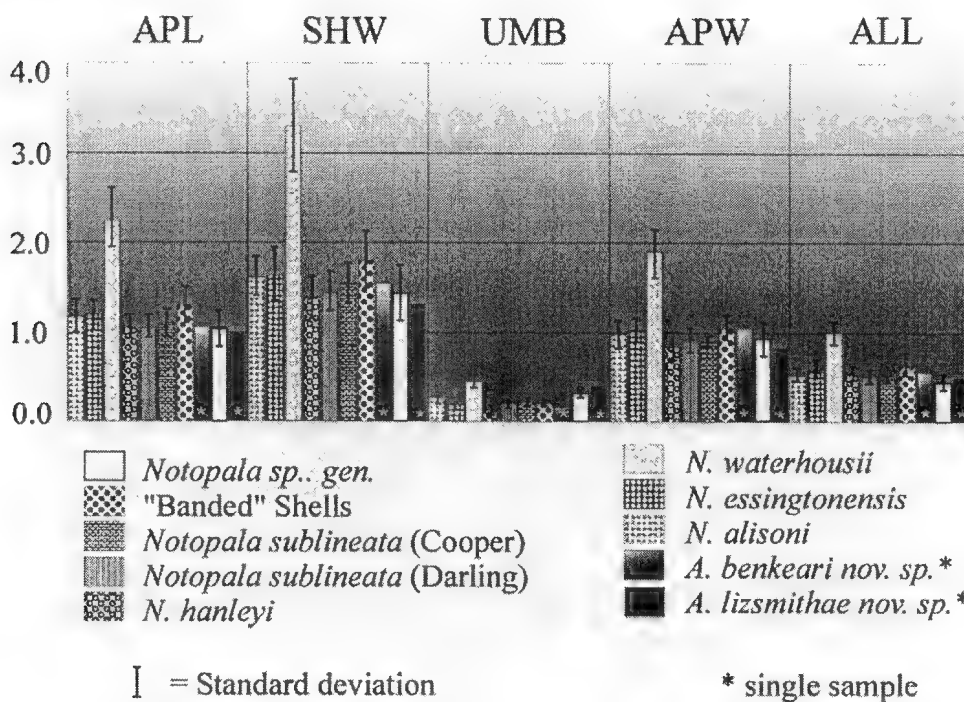


FIGURE 7. Histogram showing results of morphometric analysis. Taxa include living species of *Notopala* (modified from Sheldon & Walker 1993), *Notopala* sp. (AMF13001, AMF122185–122184), *Albianopalin benkeari* (AMF122185) and *A. lizsmithae* (AMF122186).

TABLE 1. Mean shell measurements (mm) for various living species of *Notopala* (*modified from Sheldon & Walker 1993) compared with those for *Notopala* sp. (AMF13001, AMF122185–122184), *Albianopalin benkeari* (AMF122185) and *A. lizsmithae* (AMF122186). Because not all specimens of *Notopala* sp. were complete, the number (n) of specimens used for each individual parameter is indicated separately. Standard deviation (SD) rows were not included for *A. benkeari* and *A. lizsmithae* as only a single specimen has currently been recovered for each of these taxa. Abbreviations: SHL, shell length; APL, apertural length; SHW, shell width; UMB, umbilical width; APW, aperture width; SPL, spire length; ALL, aperture lip length.

Species	Number	SHL	APL	SHW	UMB	APW	SPL	ALL
<i>*N. alisoni</i> (Brazier, 1979)	20 SD	21.59 0.086	11.91 0.039	16.3 0.054	02.59 0.014	09.77 0.034	14.78 0.064	05.35 0.015
<i>*N. essingtonensis</i> (Frauenfeld, 1862)	20 SD	21.70 0.082	12.00 0.038	16.58 0.067	1.96 0.016	10.10 0.038	14.47 0.067	6.11 0.025
<i>*N. waterhousii</i> (Adams & Angus, 1864)	10 SD	38.59 0.209	22.84 0.105	33.14 0.164	4.63 0.024	18.88 0.087	25.01 0.131	10.02 0.043
<i>*N. hanleyi</i> (Frauenfeld, 1862)	42 SD	16.67 0.520	10.50 0.026	13.83 0.036	1.29 0.00	8.52 0.025	11.00 0.037	5.57 0.013
<i>*N. sublineata</i> (D) (Conrad 1850)	28 SD	18.32 0.063	10.84 0.024	14.53 0.040	2.05 0.012	9.21 0.026	12.04 0.039	5.24 0.016
<i>*N. sublineata</i> (C) (Conrad 1850)	35 SD	19.46 0.058	11.06 0.027	15.52 0.039	2.21 0.010	8.89 0.018	12.59 0.040	4.93 0.009
<i>*'Banded' shells</i>	15 SD	22.15 0.110	13.18 0.053	18.10 0.008	2.06 0.011	10.69 0.045	14.6 0.079	6.42 0.029
<i>Notopala</i> sp.	20 SD	– –	10.35 (19) 2.563	14.43 (20) 3.053	3.24 (10) 0.616	9.20 (15) 1.80	– –	4.71 (9) 1.071
<i>A. benkeari</i>	1	17.7	10.85	16.4	3.35	9.85	–	6.2
<i>A. lizsmithae</i>	1	15.1	9.95	12.9	3.4	8.15	–	4.4

DISCUSSION

Albianopalin benkeari sp. nov., *A. lizsmithae* sp. nov. and *Notopala* sp. share the distinction of being the three oldest known definitively assigned members of the Viviparidae in Australia and thus serve to extend the range of the family in this region back to at least the uppermost Early Cretaceous. Since the family is confidently known from the Jurassic to Recent in Europe, Viviparidae therefore appears to be an ancient pre-Jurassic group of probable Pangean origin. By the Cretaceous, the family had diversified within the Gondwanan region into a range of endemic genera and species.

While there are numerous Cretaceous records of freshwater bivalves from Australia (Dettman et al 1992; Hocknull 1997; Jell & Duncan 1986; Ludbrook 1985; McMichael 1957), there are very few for non-marine gastropods from the same period. The reasons for this apparent absence are unknown, but could be related to preservational biases (with shells rapidly breaking up or dissolving after death). Another possibly reason could be a lack of gastropod species due to poor tolerance of the strongly seasonal near-freezing

climatic conditions which characterised many Australian high latitude depositional environments during the Early Cretaceous.

The implications of this study, combined with subsequent investigations, could eventually demonstrate a Gondwanan and possibly Australian radiation for many of the species living around the globe today.

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APPENDIX

Measurements (mm) of all Lightning Ridge gastropod specimens used in this study (AMF13001, AMF122166–AMF122186). Abbreviations: SHL, shell length; APL, apertural length; SHW, shell width; UMB, umbilical width; APW, aperture width; SPL, spire length; ALL, aperture lip length. Spire length measurements are omitted owing to incomplete apices in all specimens sampled.

Specimen	SHL	APL	SHW	UMB	APW	ALL
1. AMF122185 (type <i>A. benkeari</i>)	17.70	10.85	16.40	3.35	9.85	6.20
2. AMF122186 (type <i>A. lizsmithae</i>)	15.10	9.95	12.90	3.40	8.15	4.40
3. AMF13001 (<i>Notopala</i> sp.)	19.25	12.00	17.30	3.75	11.10	5.02
4. AMF122166	17.65	11.05	14.50	—	8.55	—
5. AMF122167	14.37	8.75	12.75	8.50	—	—
6. AMF122168	11.60	—	11.85	2.30	7.80	3.35
7. AMF122169	15.62	8.80	12.45	3.00	—	5.00
8. AMF122170	12.60	8.80	11.65	3.00	7.65	4.35
9. AMF122171	19.00	13.25	19.90	—	12.20	—
10. AMF122172	20.42	12.10	17.20	4.20	—	6.00
11. AMF122173	18.00	11.05	16.20	3.90	9.80	—
12. AMF122174	17.92	11.20	15.55	—	11.15	—
13. AMF122175	19.82	12.63	17.85	3.35	—	—
14. AMF122176	19.35	11.10	16.75	—	10.50	—
15. AMF122177	19.57	12.65	17.50	—	11.70	—
16. AMF122178	18.55	10.05	15.15	—	—	—
17. AMF122179	17.95	11.30	15.20	3.80	9.60	4.80
18. AMF122180	10.22	6.50	9.00	—	—	6.00
19. AMF122181	6.92	7.20	9.40	2.60	6.15	3.60
20. AMF122182	9.32	6.50	8.75	2.35	5.60	3.15
21. AMF122183	17.80	11.70	16.00	—	9.80	—
22. AMF122184	—	16.10	10.10	13.40	—	8.30

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